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Cover: Holotype of *Ausktribosphenos nyktos*. In the lower right hand corner, the holotype is superimposed on a restoration of what the living animal (body length about 85 mm) might have looked like (modelled on the erinaceid *Neotetracus sinensis*). Technical art by P. Trusler, reconstruction by D. Gelt.

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Abstract

The tribosphenic mammal *Ausktribosphenos nyktos* together with the eupantothere *Teinolophos trusleri* gen. et sp. nov. occur at the Early Aptian Flat Rocks locality in south-eastern Australia. That a eupantothere might occur in the Early Cretaceous of Australia is in accordance with previous expectations. However, quite the opposite is true of tribosphenic mammals, in particular placentals to which group *A. nyktos* may belong.

Analysis of the morphology of *Ausktribosphenos nyktos* suggests it may be (1) a placental, (2) the sister group of the placentals, or (3) a tribosphenic mammal unrelated to the placentals. On morphological grounds, the first hypothesis appears to be the most probable. Within the placentals, *A. nyktos* shows a startling resemblance to the Erinaceidae. *A. nyktos* may be characterised as having a lower dentition remarkably like that of the erinaceids set in a lower jaw which is markedly more primitive, perhaps the condition that might be found in the primitive sister-group of the Erinaceidae.

The oldest undoubted placentals known from lower dentitions are the two species of *Prokennalestes* found in the Early Cretaceous of Mongolia. If *Ausktribosphenos nyktos* is also a placental, then there are five biogeographic hypotheses divided into two main classes to explain this distribution. The first class is dispersal via Antarctica–South America–Africa–Europe and the second, direct migration between Asia and Australia. Within the first class of hypotheses, the most likely seeming variant is one which posits the extinction of placentals in South America by the Campanian after the interchange had occurred. Within the second class, a one-way transport of faunal elements from Eastern Gondwana to Asia by the mechanism of Noah's Ark type passage on a northward drifting terrane or terranes is the most likely seeming mechanism.

Introduction

In 1978, a systematic search for terrestrial vertebrate fossils in the coastal outcrops of the Early Cretaceous rocks in the Wonthaggi and Eumeralla formations in Victoria, Australia, began. This work eventually resulted in the discovery of two major sites, Dinosaur Cove in the Eumeralla Formation about 200 km to the south-west of Melbourne and the Flat Rocks site in the Wonthaggi Formation about 120 km south-east of that city (fig. 1). Although the discovery of avian and mammalian fossils was the primary objective of this work, the bulk of the material collected thus far has been dinosaurs and turtles. For the most part, these fossils are isolated bones and teeth with only two partial skeletons of dinosaurs recovered to date (Rich & Rich 1989, Rich et al. 1997).

The first mammalian specimen found in the Cretaceous of Victoria was collected in 1993 at Dinosaur Cove. In the field, the specimen was labelled as 'Turtle? humerus?' and it was not until it was completely prepared in August 1996, that it was identified as a monotreme humerus. This specimen and a fragment of a mammal tooth also recovered from Dinosaur Cove are to be described elsewhere.

On 8 March 1997, Ms Nicola Barton, a volunteer working at the Flat Rocks locality, discovered the holotype of *Ausktribosphenos nyktos* Rich et al. 1997. As a consequence of that discovery, using a binocular microscope, Mrs Lesley Kool began to re-examine systematically every fragment of bone that had been saved from that locality as well as Dinosaur Cove. As a result of that effort, three more mammalian specimens have now been recovered from the Flat Rocks locality.

Three days prior to Ms Barton's discovery, an avian furculum was found at the Flat Rocks locality. Although feathers were previously known from the contemporaneous Koonwarra locality only about 27 km from Flat Rocks (Waldman 1970), this furculum is the first osteological specimen of a Cretaceous bird from Victoria, and the first representative of this avian element ever found in the Mesozoic of Australia. It is currently being described elsewhere.

A Leica MZ8 binocular microscope was utilised to examine the fossils described here. These same specimens were collected under permits NP978/111 and NP 10000241 issued by the Victorian Department of Natural Resources and Environment, Flora and Fauna Branch.
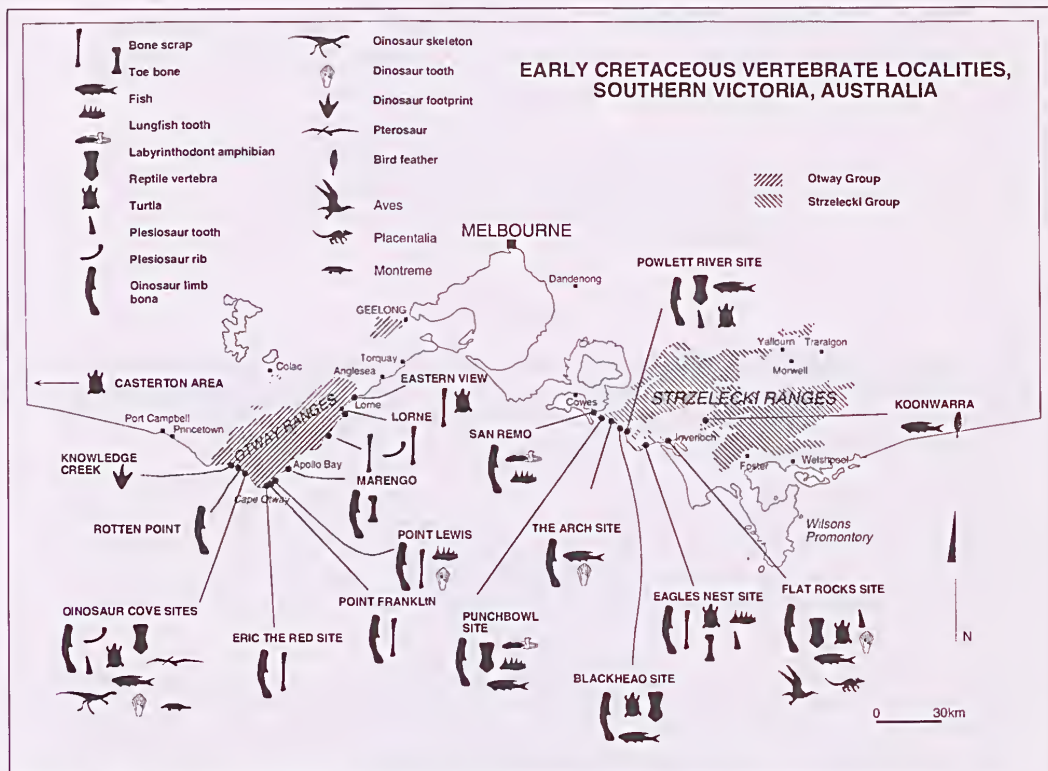
Figure 1. Early Cretaceous tetrapod sites in Victoria, Australia.

Locality, Stratigraphic Unit and Age

All the mammals described below were found at the Flat Rocks fossil vertebrate site, 38° 39' 40±02" S, 145° 40' 52±03" E (World Geodetic Standard 1984) on the shore platform of the Bunurong Marine Park, Victoria, Australia. The fossils occur in the Wonthaggi Formation, a non-marine volcaniclastic sandstone and mudstone unit approximately 3 000 m thick.

Palynological examination of five mudstone samples collected from a 7 m thick floodplain sequence immediately underlying the Flat Rocks vertebrate fossil site indicates it is *Pilosisporites notensis* Zone (Aptian) in age (see fig. 2). This age determination is based on the presence of the spore *Pilosisporites notensis* in one of the five mudstone samples examined. This spore makes its first appearance in Australia at the base of the Aptian (Morgan 1980) and continues up into the Albian (Helby, Morgan & Partridge 1987). The site is not Albian in age because none of the samples examined contained any spore or pollen species which make stratigraphically younger first appearances within the overlying *Crybelosporites striatus*, *Coptospora paradoxa*, or *Phimopollenites pannosus* spore-pollen zones.

The Aptian age determination for the Flat Rocks vertebrate fossil site is supported by the fission track dating of detrital zircons obtained from a volcaniclastic sandstone 50 cm above the bone-bearing conglomerate. The 21 analysed zircons yielded a pooled age of 122.5±8 Ma (1σ) with a chi-squared probability of 99.7%. The pooled age represents the age of the source volcanic rocks, because vitrinite reflectance measurements of coalified plant fragments from the site indicate that the sediments have not experienced burial temperatures greater than 77°C. This is well below the partial annealing temperature for zircon (200°C), which indicates they have not been thermally annealed. This interpretation substantiates an earlier fission track study by Green (1989) on detrital zircon from similar volcaniclastic sandstones of *Crybelosporites striatus* Zone age in the Otway Basin approximately 130 km to the west of Flat Rocks. Green (1989) obtained a pooled fission track age that overlapped its chronobiostratigraphic age. This overlap suggests the lag time between eruption, erosion, transport, and deposition was probably in the order of a few million years. The pooled age for Flat Rocks, therefore, suggests the site is probably situated close to the base of the Aptian, which ranges in age, according to the time scale of Gradstein et al. (1994), from 121 to 112.5 Ma.
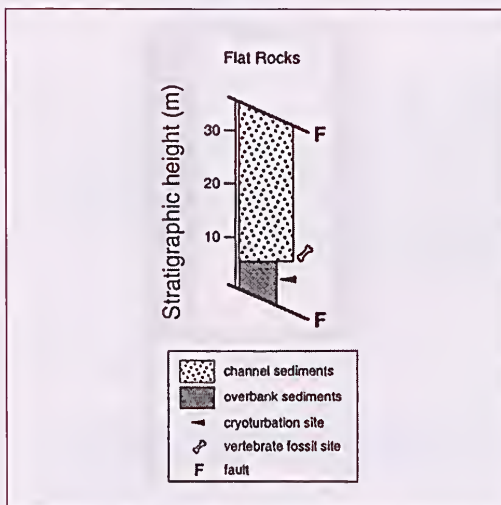
Palaeoenvironment

Constantine et al. (1998) presented evidence for the occurrence of cryoturbation structures 3 m stratigraphically
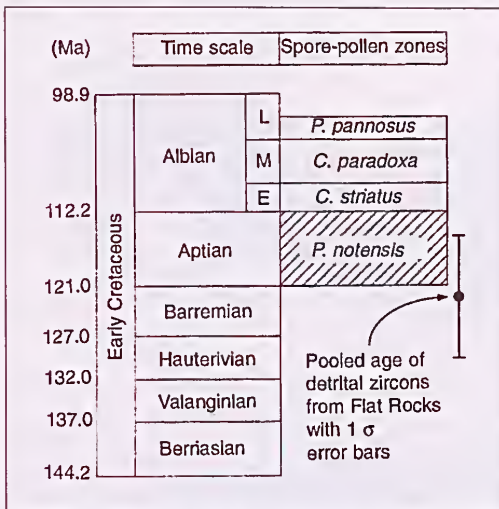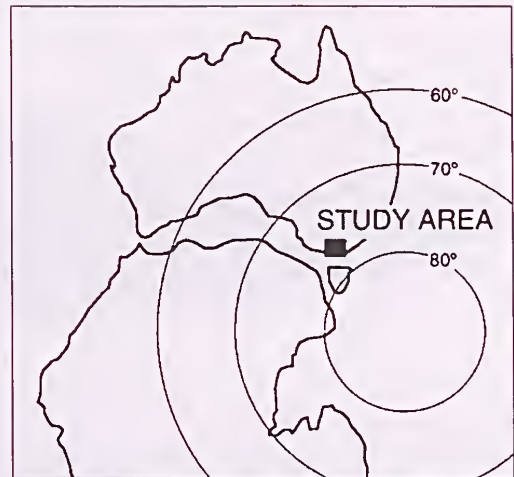
Figure 2. Age of the Flat Rocks vertebrate fossil site (hatched) relative to the geologic time scale (Gradstein et al. 1994). Spore-pollen zones modified after Helby, Morgan and Partridge (1987). From Rich et al. (1997).

Figure 4. Position of south-eastern Australia relative to Antarctica and the South Pole during the Aptian–Albian (Early Cretaceous).
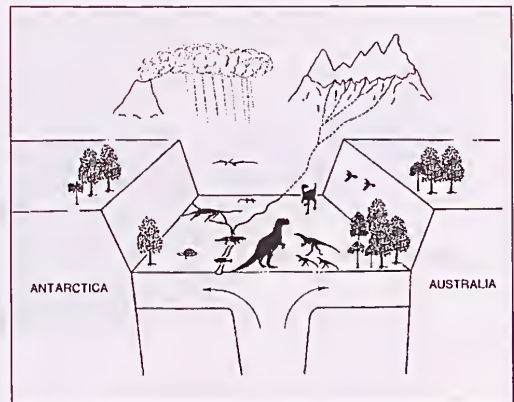

Figure 3. Simplified stratigraphic column showing the relationship between the Flat Rocks fossil locality and the cryoturbation site 3 m below it. Modified from Constantine et al. (1998).

Figure 5. Cross section from south-eastern Australia to East Antarctica in the Early Cretaceous. Separation between the two continents began in the Late Jurassic with the initiation of a spreading centre which resulted in a rift valley being formed on the common boundary of the two continental plates. Into this rift valley poured a vast quantity of volcanogenic sediments derived from volcanoes which were perhaps to the east in the vicinity of the Lord Howe Rise (Bryan et al. 1997) or to the south along the axis of the rift valley (Felton 1997a-b). Large rivers flowed across the floor of this rift valley. They were fed perhaps in part by meltwater of snow, presumably located at high altitude on mountains along the margins of the rift valley or the volcanoes which produced the volcanogenic sediments. The Early Cretaceous tetrapod and plant fossils primarily occur in sediments that were laid down in small streams which flowed into the larger rivers on the floor of the rift valley. Subsequent to the Early Cretaceous, the sediments which had been deposited on the floor of the rift valley were lithified as they were buried under additional sediment. Then late in the Cainozoic, these sediments were uplifted to form the Strzelecki and Otway Ranges.
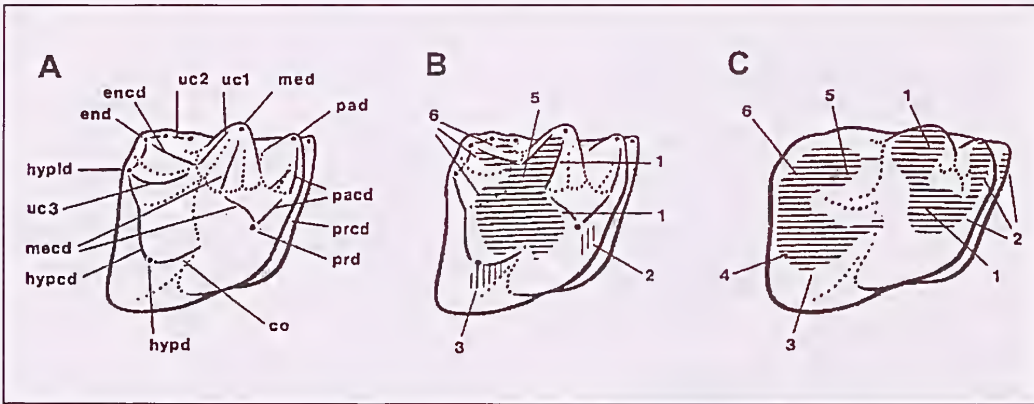
below the fossiliferous unit at the Flat Rocks site, where the mammals described here were found. These cryoturbation structures imply seasonally frozen ground was present there during the Aptian (fig. 3). That, plus other evidence they presented, suggests a mean annual palaeotemperature between -2°C and +3°C for the area. This accords well with a previous estimate of the mean annual temperature based on the oxygen stable isotope geochemistry of carbonate concretions (± 5°C, Gregory et al. 1989) but contradicted earlier palaeobotanical evidence suggesting a mean annual temperature for the area of 8–10°C (Parrish et al. 1991).

Figure 6. (a) Generalised lower molars of *Ausktribosphenos nyktos*. Abbreviations: **co**, cristid obliqua; **encd**, entocristid; **end**, entoconid; **hypld**, hypoconulid; **hypcd**, hypocristid; **hypd**, hypoconid; **mecd**, metacristid; **med**, metaconid; **pad**, paraconid; **pacd**, paracristid; **prcd**, precingulid; **prd**, protoconid; **uc1**, unnamed cristid 1; **uc2** unnamed cristid 2; **uc3**, unnamed cristid 3. (b) Restoration of the wear surfaces on the lower molars of the holotype of *A. nyktos*, MSC 007. (c) Wear surfaces on the M_{1-2} of MSC 145, referred specimen of *A. nyktos*. Note that the degree of wear in MSC 145 is generally significantly greater than on MSC 007 in most but not all areas.

In the Early Cretaceous, Australia was located at a high southern latitude (fig. 4) and still joined with Antarctica. The two continents were in the initial stages of rifting apart. In the Strzelecki and Otway ranges on the southern coast of Victoria, occur thick deposits of volcaniclastic sediments laid down at this time in the rift valley that formed as the two continents separated (Dettmann et al. 1992, Frakes et al. 1987) (fig. 5). Braided rivers cut across the floor of this rift valley. It was in the bed of one of the lesser tributary streams of such a river that the fossils found at the Flat Rocks site accumulated, probably as the result of a series of discrete flood events which caused the accumulation of mud clasts and plant debris, together with isolated bones and teeth (Vickers-Rich & Rich 1997).

Institutional Abbreviations

AM F   Palaeontology Collection, Australian Museum, Sydney, Australia

F:AM   Frick Collection, American Museum of Natural History, New York, United States of America.

MSC   Monash Science Centre, Clayton, Victoria, Australia.

NMV P Palaeontology Collection, Museum Victoria, Melbourne, Australia.

UCM   University of Colorado Museum, Boulder, Colorado, United States of America.

Systematics

Class Mammalia Linnaeus 1758
Subclass Theria Parker and Haswell 1897
Infraclass Placentalia Owen 1837
Order Ausktribosphenida Rich et al. 1997
Family Ausktribosphenidae Rich et al. 1997
Ausktribosphenos Rich et al. 1997

Type species. Ausktribosphenos nyktos Rich et al. 1997

Diagnosis. Distinguished from the Monotremata (Archer et al. 1978, 1985, 1992, 1993, Flannery et al. 1995) by (a) presence of a paraconid on M_1 and all trigonids

relatively anteroposteriorly expanded, (b) well-developed tribosphenic pattern of wear on lower molars, particularly within the talonid basin as well as external to it (fig. 6), (c) P_4 with three trigonid cusps and trigonid sub equal in size to that of M_1, (d) except for *Tachyglossus aculeata* with its highly reduced dentary, absence of a masseteric canal and masseteric foramen, and (e) absence of an internal coronoid process.

Distinguished from Aegialodontidae (*sensu* Fox 1980) by (a) more anteroposteriorly compressed molar trigonids and (b) the lack of a distal metacristid (*sensu* Fox 1975) on M_{1-3}.

Distinguished from Pappotheriidae (*sensu* Fox 1980) by (a) the lower trigonid cusps on the molars and (b) on the M_1, the talonid width being as great or greater than the trigonid width.

Distinguished from the Marsupialia and Deltatheroida (*sensu* Kielan-Jaworowska & Nessov 1988) by (a) P_4 with all three trigonid cusps well-developed, (b) the presence of three, rather than four, lower molars and at least four, rather than three, lower premolars, P_5 submolariform rather than premolariform, and (d) except for *Caluromys, Dactylopsila, Myrmecobius, Phascolarctos* and *Tarsipes* (Sánchez-Villagra & Smith 1997), absence of an inflected angle on the dentary.

Figure 7 (Opposite). Holotype of *Ausktribosphenos nyktos*, MSC 007 [= NMV P208090]. Maximum length of specimen, 16 mm. (a) Labial view, (b) Occlusal view, (c) Lingual view, (d) Ventral view, (e) Anterior view, (f) Posterior view, Technical art by P. Trusler.
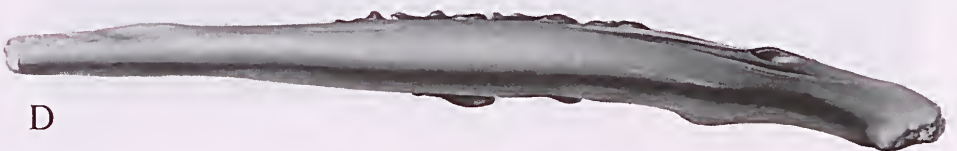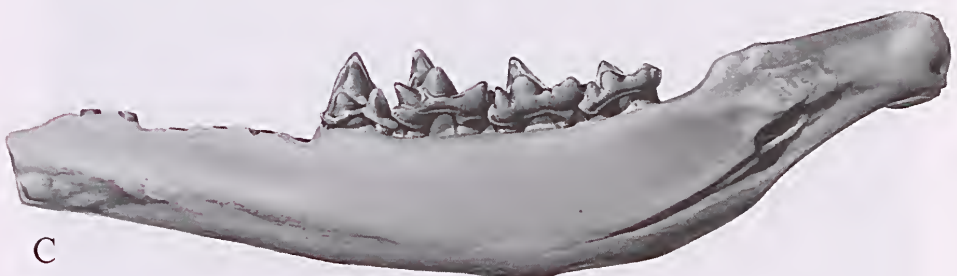
Figure 8. Stereophotographs of the holotype of *Ausktribosphenos nyktos*, MSC 007 [= NMV P208090]. (a) Lateral view, (b) Occlusal view. X8.00.
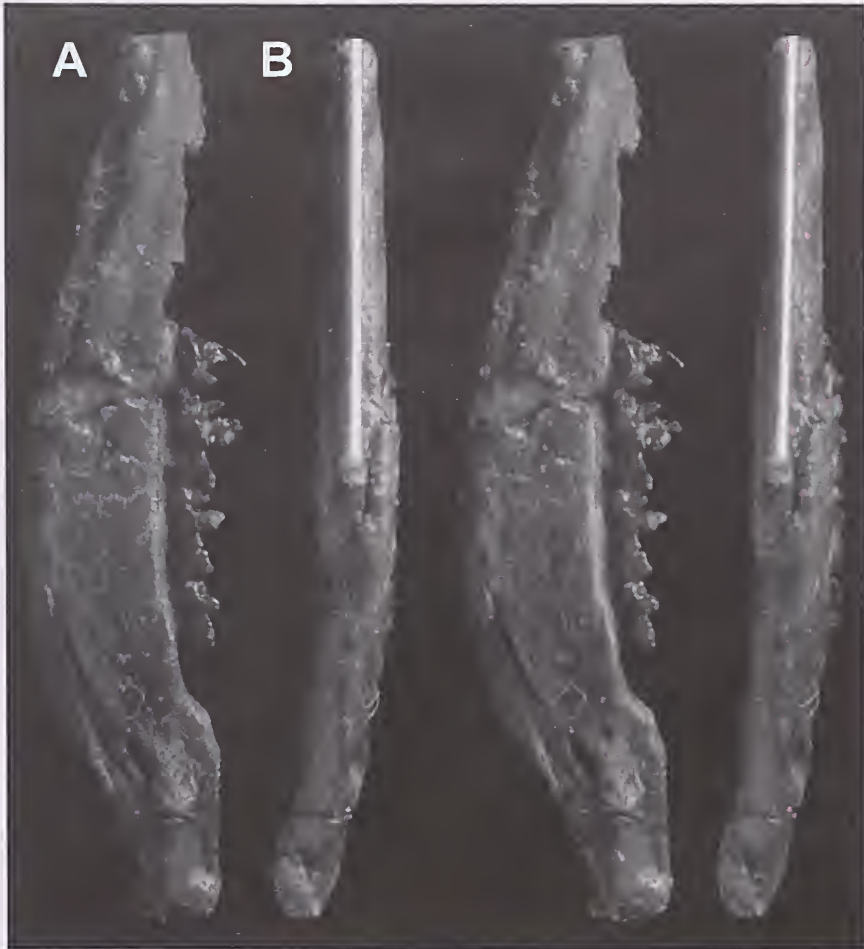
Figure 9. Stereophotographs of the holotype of *Ausktribosphenos nyktos*,
MSC 007 [= NMV P208090]. (a) Lingual view, (b) Ventral view. X7.75.

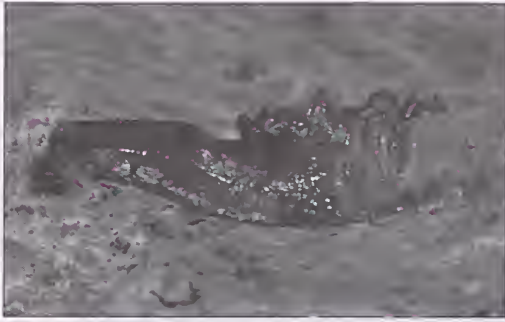**Figure 10.** The posterior part of the holotype of *Ausktribosphenos nyktos*, MSC 007 [= NMV P208090], as it appeared when partially excavated from the rock in which it had been embedded.

Distinguished from the Marsupialia by lack of a posterolabial cingulum on M_{1-3}.

Distinguished from the Deltatheroida (*sensu* Kielan-Jaworowska & Nessov 1988) by (a) strong, well-developed talonids, (b) strong precingulids, and (c) paraconids lower than metaconids on M_{1-3}.

Distinguished from all other Placentalia including *Prokennalestes* by (a) the presence of a remnant of the surangular facet (Kielan-Jaworowska & Dashzeveg 1989), (b) a crest on M_{1-2} linking the hypoconulid and metaconid buccal to the entoconid, which is separately linked to the metaconid. Distinguished from most other Placentalia by the close proximity of the hypoconulid to the entoconid on the lower molars.

Distinguished from all other Placentalia except *Prokennalestes* by the presence of (a) remnants of a Meckelian groove and (b) the coronoid bone on the lingual side of dentary.

Distinguished from *Prokennalestes* but similar to many more advanced placentals by (a) the much smaller size of the M_3 relative to M_{1-2}, (b) the lower trigonid cusps on M_{1-3}

relative to tooth length, (c) the presence of four double-rooted lower premolars instead of five, (d) the presence of a single rather than double-rooted C_1, or the presence of a single rather than double-rooted P_1 (Sigogneau-Russell, Dashzeveg & Russell 1992), and (e) the lack of a labial mandibular foramen.

Ausktribosphenos nyktos Rich et al. 1997

Holotype: MSC 007 [= NMV P208090]. Right mandible fragment only slightly crushed with P_5-M_3 plus eight alveoli anterior to P_5, area of condyle abraded, remnant of base of angular process preserved, base of ascending ramus preserved (figs 7–10).

Referred material: MSC 145 [= NMV P208228]. Right mandible fragment moderately crushed with P_4-M_2, four tooth roots present anterior to P_4, angular process present, base of ascending ramus preserved (figs 11–13). The talonid of the M_2 of this specimen broke up during preparation. Fortunately, a mould of most of the crown of this tooth was made by Dr Donald E. Russell prior to that event (fig. 11a).

Diagnosis: That of the genus until other species are described.

Description: No foramina are present on the labial side of the dentary. The base of the masseteric fossa is preserved with the anterior edge bounded by a sharp vertical ridge, whereas the ventral margin is more rounded.

As preserved, the symphysial region is confined to the lower half of the lingual side of the jaw beneath the posterior root of P_3.

Figure 11 (Opposite). Stereophotographs of referred jaw of *Ausktribosphenos nyktos*, MSC 145, [= NMV P208228]. (a) Partial cast of M_2. Mould poured by Dr Donald E. Russell prior to original specimen suffering damage to talonid. X7.61. (b) Lateral view. (c) Occlusal view. X8.42.

Measurements (in mm) of *Ausktribosphenos nyktos*						
	Total Length		Trigonoid Width		Talonoid Width	
	MSC 007	MSC 145	MSC007	MSC 145	MSC 007	MSC 145
P_5	1.4	1.4	1.2	1.1		
M_5	1.6	2.3	1.4	1.4	1.7	1.4
M_2	1.8	2.3*	---	1.7	---	1.3*
M_3	1.2	---	0.9	---	0.9	---
*Measurements of cast						
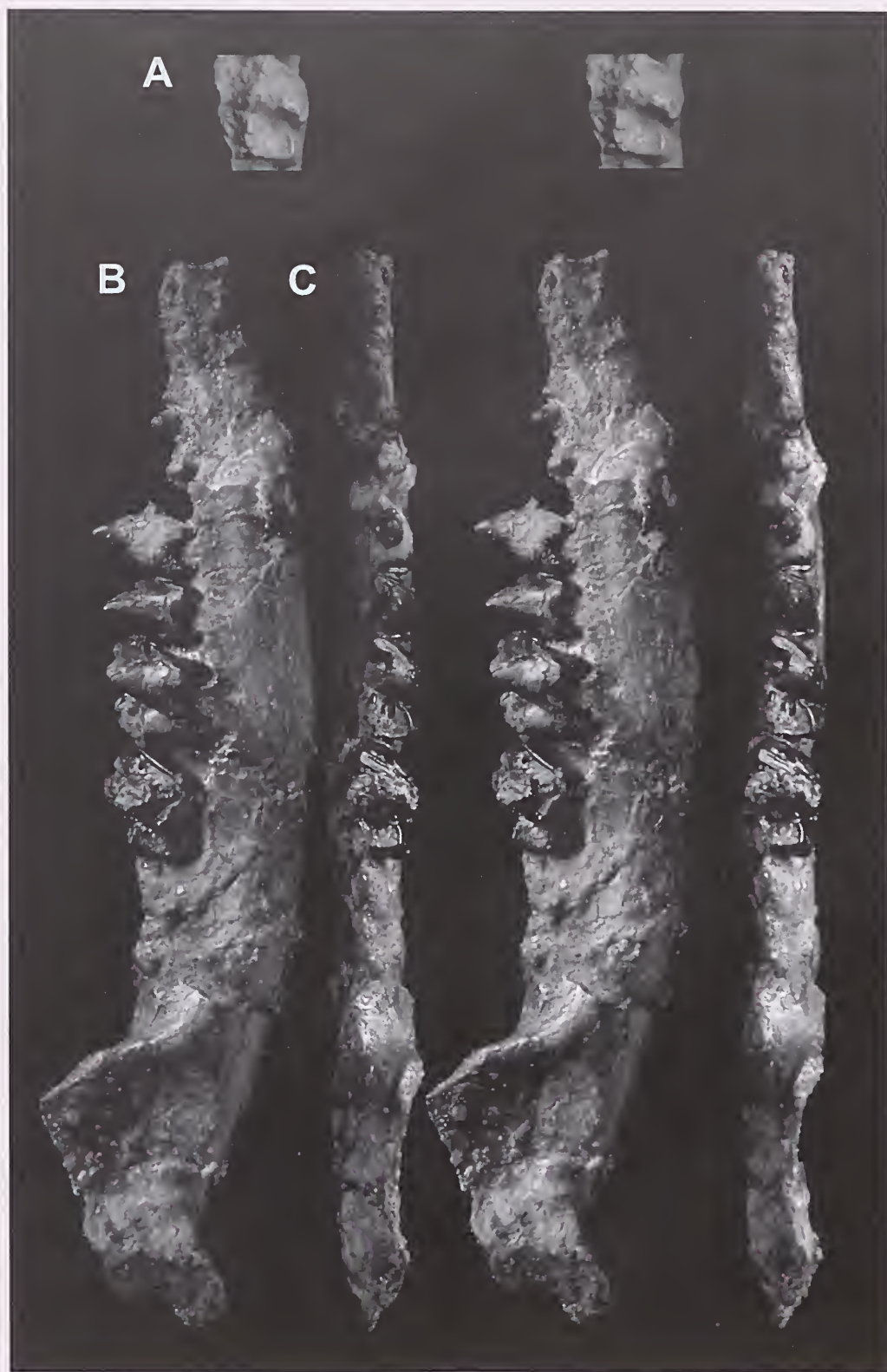
On MSC 007, a distinct Meckelian groove is developed from beneath M_3 posteriorly to the mandibular foramen from which it is separated by a narrow ridge. A shallow depression, the surangular facet, presumably a vestigial remnant of a groove for a post dentary bone, begins anteriorly at a point just beneath and anterior to the posteriorly facing mandibular foramen as well as below the posterior end of the Meckelian groove from which it is clearly separated. This shallow depression extends posteriorly to a point near the anterior edge of the base of the mandibular process. This depression has been slightly affected by crushing, which may have made it more prominent than it originally was. A small condylar foramen is developed near the preserved posteroventral corner of the jaw.

On MSC 145, there may be a trace of the Meckelian groove preserved just anterior to the mandibular foramen. Anterior to this point, the specimen is damaged to such an extent that it is impossible to say whether or not a Meckelian groove was once present. The separation of the mandibular foramen from the surangular facet is much broader than in MSC 007. The surangular facet terminates posteriorly about halfway between the mandibular foramen and the base of the angular process. No condylar foramen is preserved on MSC 145.

Only the base of the ascending ramus is preserved on MSC 145. What remains suggests that the anterior edge was nearly vertical, rather than posteriorly inclined. At its anterior end is a rugose area, presumably the site where the coronoid bone was located. Posterior to that can be seen a horizontal ridge that lies above both the mandibular foramen and the surangular facet.

P_{1-3}. Only the roots of these teeth are preserved on MSC 007. On that basis, they seem to have been mediolaterally compressed teeth noticeably narrower than the P_{4-5}. P_1 had a single root, whereas P_{2-3} were double-rooted. On MSC 145, owing to breakage of the jaw immediately anterior to P_4, it is uncertain to which teeth the four visible roots in that region should be assigned.

On all five teeth known, P_4-M_3, the crowns are cantilevered well beyond the underlying roots on both the labial and lingual sides.

P_4. On the one specimen where this tooth is preserved [MSC 145], the break in the rock that exposed the specimen passed through the tooth. Among other things, the break destroyed the metaconid (if it was present) and damaged the paraconid. But, what remains is quite similar in form to the better known P_5, the only difference being that the P_4 is slightly narrower.

P_5. This tooth consists primarily of a trigonid with the protoconid much higher than the metaconid and the paraconid being slightly lower and smaller. A distinct precingulid is developed from the labial corner of the base of the prevallid almost to its lingual corner. A postcingulid is developed along the base of the postvallid instead of a full-fledged talonid. No talonid cusps are present.

M_1. The protoconid is the tallest of the trigonid cusps with the metaconid slightly lower and the paraconid the lowest of all. There is a definite carnassial notch present in the paracristid. The metacristid is too damaged [MSC 007] or encrusted with matrix [MSC 145] in the expected area of a notch to ascertain if a carnassial notch was present. A precingulid is developed along the entire length of the base of the prevallid. The hypoconid is lower than the entoconid. Damage and wear to the talonids on both available specimens of the M_1 is extensive, but what remains suggests it was rather similar to those of the M_2's which are somewhat better preserved in both specimens in this area. Although the width of the talonid of MSC 007 (given in the Table of Measurements) is 0.3 mm greater than the trigonid width, damage to the talonid makes this measurement suspect. It may well be that this tooth, prior to being damaged, resembled the M_1 of MSC 145 in having the trigonid and talonid within 0.1 mm of being equal.

M_2. This tooth is slightly longer and the trigonid slightly wider than on M_1. The corresponding trigonid cusps are slightly lower than those on the M_1. Except that the paraconid is smaller relative to the size of the metaconid, the trigonid cusps have the same relative proportions to one another as they do on that tooth. Likewise, the precingulid is equally developed. On the talonid, the hypoconid is lower than the entoconid, as is the case on the M_1. A prominent cristid (*uc1*, unnamed cristid 1, fig. 6a), descends the posterior side of the metaconid and extends towards a similar entocristid directed forward from the entoconid. Unnamed cristid 1 is not a distal metacristid (*sensu* Fox 1975), because it is nowhere close to the cristid obliqua. Lingual to the entocristid and subparallel to it is a second, higher cristid (*uc2*, fig. 6a) extending forward from the entoconid along the lingual margin of the tooth. Along the length of this cristid are one or two small cuspules, the one at the anterior end being the most distinct. Between these two cristids extending in parallel forward from the entoconid is a small basin partially cut off from the rest of the talonid basin. The same pattern may have been present on M_1, but was obliterated by wear in both available specimens. The hypocristid is preserved on the M_2, being much lower than the hypoconulid and convex posteriorly in occlusal view. Extending forward into the talonid basin from the hypoconulid is an arcuate cristid (*uc3*, fig. 6a) that parallels the base of the entoconid, continuing to a point where it joins the posterior cristid from the metaconid and the entocristid from the entoconid. The cristid *uc3* appears to

Figure 12 (Opposite). Stereophotographs of referred jaw of *Ausktribosphenos nyktos*, MSC 145, [= NMV P208228]. (a) Lingual view, (b) Ventral view. X9.06.

Figure 13. Referred jaw of *Ausktribosphenos nyktos*, MSC 145, [= NMV P208228], as it appeared when partially excavated from the rock in which it had been embedded.

have also been present on M_1. However, in the case of MSC 007, the lingual area of the talonid of this tooth was heavily damaged when the rock in which the fossil was preserved was broken open. In the case of the M_1 of MSC 145, this same area of M_1 is rather worn. The cristid obliqua extends anterolingually from the hypoconid and terminates posterior to the tip of the protoconid, a short distance behind the postvallid.

M_3: This tooth is markedly smaller than either the M_1 or M_2. The metaconid is only slightly lower than the protoconid, and the two cusps are subequal in size. The paraconid is much smaller and lower than the metaconid, the relative difference in size being even greater than in the case of M_1 or M_2. Lingually, the precingulid is as wide in absolute terms as that of M_1. Labially, the precingulid disappears at the point of contact with the M_2.

The talonid is completely enclosed by a continuous crest with slight swellings indicating the positions of the entoconid and hypoconulid. The hypoconulid is posterolingual to the entoconid. The hypoconid is a more prominent cusp. On the posterolabial margin of the tooth, there is no cingulum flanking the hypoconid. The cristid obliqua, preserved without a flaw, extends anterolingually from the hypoconid and terminates posterior to the tip of the protoconid a short distance behind the postvallid.

Molar wear facets. With broad talonid basins on the lower molars that show clear evidence of wear on the labial side of the entoconid (Crompton's (1971) wear facet 6) and as well as on the lingual side of the cristid obliqua, *Ausktribosphenos nyktos* appears to have had a prominent protocone on its upper molars, and, therefore, can be considered a tribosphenic mammal *sensu* Simpson (1936) (fig. 6).

On the M_{1-2} of the holotype of *Ausktribosphenos nyktos*, MSC 007, there is a wear surface on the labial side of the entoconid that lies in the same plane as one on the crests which arcs around the labial side of that cusp. Presumably, the two wear facets together are the

functional equivalent of the single wear surface 6 of Crompton, seen on the lingual side of the entoconid in tribosphenic molars (Crompton 1971). In addition, there is a third wear facet on the entocristid, which, although not in exactly the same plane as the first two wear facets, may also be wear facet 6. This well-developed wear surface passes without an apparent break into the bottom of the talonid basin and onto the postvallid, where it is equally strong. Although, presumably, these latter wear surfaces are homologous with wear surfaces 5 and 1, respectively, of Crompton, there are no evident boundaries between them. Some evidence of wear surface 2 may be present on the anterior slope of the protoconid of M_1, but there is only the slightest evidence of wear surface 3 and none of wear surface 4 on the anterior and posterior sides, respectively, of the hypoconid. This distribution of wear facets is what might be expected of a fully tribosphenic mammal in which the unknown upper molars had prominent protocones with major wear surfaces on their tips as well as on their anterior and posterior slopes. In addition, these upper molars had well-developed wear surfaces on the paracrista (wear surface 1a of Crompton) and/or preparaconule crista (wear surface 1b of Crompton). Unlike M_{1-2}, the only available M_3 is not damaged. Wear facets 1, 5 and 6 of Crompton are present, but more subdued than on M_{1-2}. There is no sign of wear facets 2–4 on M_3.

For the most part, the degree of wear on the molars of MSC 145 is noticeably greater than on MSC 007. For example, wear surface 2 is well developed on MSC 145. Also, the hypoconid on MSC 145 is worn flat, so that the areas where wear surfaces 3 and 4 would be expected are part of one continuous, horizontal wear surface. This horizontal wear surface passes into the near vertical wear surface 6 without a sharp break between them. Likewise, wear surface 6 on MSC 145 passes into wear surface 5 without a clear break between them as is the case in MSC 007. There is no obvious wear surface near the base of the prevallid on MSC 145. This is surprising because this area of wear facet 1 is quite distinct on MSC 007. In stark contrast, near the tips of the protoconid and metaconid, wear facet 1 is far more heavily worn on MSC 145 than on MSC 007.

The pattern of wear on the molars of *Ausktribosphenos nyktos* is quite unlike the penecontemporaneous Cretaceous monotreme *Steropodon galmani*. Wear in the talonid region of the lower molars of *S. galmani* is confined to the labial side of the cristid obliqua, that is, to Crompton's wear facets 3 and 4 (Kielan-Jaworowska, Crompton, & Jenkins 1987). It was this feature which prompted Kielan-Jaworowska, Crompton, and Jenkins (1987) to remove *S. galmani* from the Tribosphenida on the basis that it did not have a tribosphenic dentition.

Discussion. Although MSC 145 is about one-third larger than MSC 007, the two are here provisionally regarded as representatives of a single species. Other than size, there are no morphological differences between the two

Figure 14. The erinaceid *Untermannerix copiosus* Rich 1981, F:AM 76703 (holotype), Central Pojoaque Bluffs, New Mexico, United States of America (35° 55' 11" N, 106° 02' 31" W), Pojoaque Member of the Tesuque Formation, Barstovian or Clarendonian (Late Miocene – Early Pliocene). (a) Lingual view of left mandible, (b) Occlusal view of left mandible, (c) Lateral view of left mandible, (d) Occlusal view of right mandible. X4.5. Figure 7 in Rich (1981), used with permission of the American Museum of Natural History.

specimens which are clearly owing to causes other than post-mortem damage. In particular, because of the damage done to MSC 007 in the process of its discovery, it is difficult to ascertain how much of the quite evident proportional differences in the length and width of the M_{1-2} between that specimen and MSC 145 is owing to that factor and how much to innate dissimilarity.

Based on the published evidence, there would appear to be two additional differences between *Ausktribosphenos nyktos* and the monotremes: the number of premolars and the number of molar roots. However, there is an edentulous mandible from Lightning Ridge, New South Wales, AM F97263, which is probably referable to the monotreme *Steropodon galmani* and which, like *A. nyktos*, has more than two premolars, and the molars have only two roots. The latter feature can also be seen on the holotype of *Steropodon galmani*.

Among tribosphenids, as indicated in the diagnoses, *Ausktribosphenos nyktos* is clearly not a deltatheroid (*sensu* Kielan-Jaworowska & Nessov 1988), marsupial, nor tribothere (*sensu* Fox 1980). The characters mentioned in the diagnoses coupled with a post-incisor dental

formula of C1, P1–4 or P1–5, M1–3, are a combination of features unknown other than in placentals among the tribosphenids and highly characteristic of them (Clemens & Lillegraven 1986). This is the basis for regarding *A. nyktos* as a placental.

Except for the presence of a remnant of the Meckelian groove and indications of a vestigal coronoid bone, features it shares with the undoubted placental *Prokennalestes* (Butler 1990, Cifelli 1993, Kielan-Jaworowska & Dashzeveg 1989), plus the presence of a surangular facet, *Ausktribosphenos nyktos* is a rather advanced Cretaceous placental. Advanced features include the posterior position of the base of the angular process, the marked reduction in the size of the M_3 relative to M_{1-2}, the reduced height of the molar trigonids relative to tooth length, and the width of the M_1 talonid being as great or greater than the trigonid.

A unique feature of *A. nyktos* is that there is a linkage between the hypoconulid and metaconid which bypasses the entoconid, in the form of a crest that arcs around the labial side of the base of the entoconid. It is this autapomorphy alone which forms the basis for the recognition of the Order Ausktribosphenida.

The form of the P_5 of *Ausktribosphenos nyktos* is unusual, but not unknown, in other placentals. Some erinaceids also have a well-developed trigonid and merely a posteingulum, instead of a full-fledged talonid on their most posterior lower premolar (Butler 1948, Rich 1981) (fig. 14).

If, for a moment, the hypothesis that *Ausktribosphenos nyktos* is a placental is accepted, the next question that arises is to which group or groups among the known Placentalia might *A. nyktos* be closest? In their review of the Erinaceomorpha, Novacek, Bown, and Schankler (1985) list a number of features of the dentition characterising both the Erinaceomorpha and within them, the Dormaalidae, Amphilemuridae and Erinaceidae. By all their dental criteria, *A. nyktos* would appear to be a member of the Erinaceomorpha and, within that group, an erinaceid. However, there are three features of the lower jaw that distinguish *A. nyktos* from all members of the Erinaceomorpha: presence of a Meckelian groove, a facet for the cornoid bone, and shallow, vestigial groove for a post-dentary bone (= surangular facet).

The following features of the dentition of the Erinaceomorpha listed by Novacek, Bown, and Schankler (1985) are shared with one or both specimens of *Ausktribosphenos nyktos*: P_4 with a short, unbasined talonid lacking cusps; molar paraconids compressed. 'Molar trigonid cusps lower, less sectorial, and more anteriorly canted than in *Kennalestes, Cimolestes, Procerberus, Asioryctes,* palaeoryctids (*sensu stricto*), primitive leptictids (e.g. *Prodiacodon*), geolabidids, early miacids, and creodonts,' (p. 3). M_{1-2} talonids wider than trigonids; molars with high entoconids and low hypoconids often flattened in early stages of wear. On

Figure 15. The erinaceid *Entomolestes grangeri* Matthew 1909, UCM 57495, UCM locality 92180, Bridger Basin, Uinta County, Wyoming, United States of America. Henry's Fork White Layer which is 50–100 cm above the Henry's Fork Tuff, approximately two-thirds the way up in unit C of Matthew (1909), Bridger Formation, Bridgerian (Middle Eocene). X7.50

This specimen displays a number of significant similarities with the dentition of *Ausktribosphenos nyktos*. Among them are the heights and orientation of the M_1 cusps, namely the profiles of the entoconid, paraconid and metaconid in lingual view, the paraconid pointing anterodorsally, the orientation of the cristid obliqua, lingual position of the hypoconulid resulting in its being 'twinned' with the entoconid and the separation of these two cusps by a cleft. Other dental similarities are the disposition of labial trigonid cingula and the degree of anteroposterior expansion of the trigonids on both P_5 and M_1, together with the lack of a cingulum on the posterobuccal corner of the M_1.

Notable differences between *Entomolestes grangeri* and *Ausktribosphenos nyktos* are the presence of three lingual crests on the molar talonids of *A. nyktos* (entoeristid, unnamed cristid 2, unnamed cristid 3) while there is only the entocristid on *E. grangeri*, wider talonid and higher paraconid and metaconid on the P_5 of *E. grangeri*, and lack of Meckelian Groove, surangular facet, and facet for coronoid bones on the lingual surface of the mandible of *E. grangeri*.

MSC 145, the talonid of M_1 is equal to the trigonid in width whereas on the M_2, it is noticeably narrower (see figures 11a and 11e).

The following features of the Erinaceidae listed by Novacek, Bown, and Schankler (1985) are shared with *Ausktribosphenos nyktos*: progressive reduction in molar size from M_1 to M_3; molars semi-rectangular in outline with some degree of exodaenodonty (i.e. bases of the trigonid and talonid cusps are significantly lower on the labial than lingual side of the posterior premolars and anterior molars); M_1 paraconid salient and anteriorly projecting, elongating the prevallid shearing wall; and hypoconulids markedly reduced on M_{1-2}.

Novacek, Bown and Schankler (1985) candidly discussed the difficulty of determining the polarity of many of the characters mentioned in the three paragraphs above and the assessment of their phylogenetic significance, noting the following in the preface to their analysis of the Erinaceomorpha.
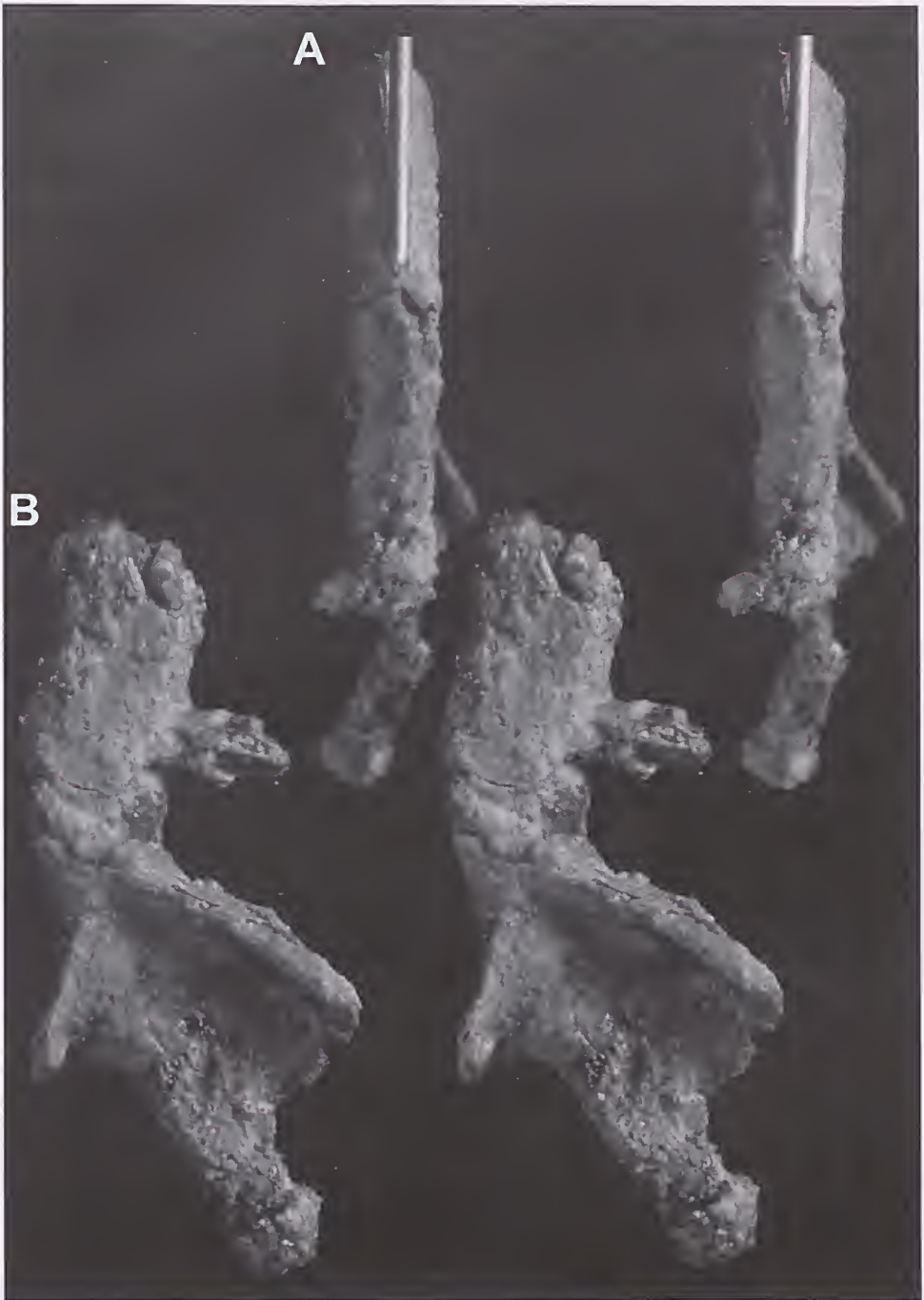
Figure 16. Stereophotographs of the holotype of *Teinolophos trusleri*, MSC 148, [= NMV P208231].
(a) Ventral view, (b) Lateral view. X9.01.

'The above characterization of the Erinaceomorpha is discussed at length by Novacek (1982). Polarity assessments of tooth characters in early insectivorans are difficult, owing to the often subtle differences observed among these taxa. Only the combination of the above cited features serves to distinguish erinaceomorphs; no single feature is by itself diagnostic. Readers familiar with the problem will be aware of other early eutherians that share at least some of these traits (see also Novacek, 1982). Nevertheless, the diagnosis is useful if it is assumed that high-cusped, sectorial molars and premolars seen in early leptictids, palaeoryctids, and a variety of Cretaceous eutherians represent a closer approximation of the primitive eutherian morphotype.'

This admonishment is valid and many of the features Novacek, Bown and Schankler (1985) enumerated could not be assessed in the available specimens of *Ausktribosphenos nyktos*. Therefore, the known similarity between the dentitions of *A. nyktos* and the Erinaceomorpha and with the Erinaceidae in particular (see figures 14–15), should at this stage of knowledge be regarded as a tantalising hint as to the possible position of *A. nyktos* within the Placentalia. There is not unequivocal evidence that *A. nyktos*, with its plesiomorphic mandibular structure together with its apomorphic dentition, is the primitive sister-group of the Erinaceidae.

It has been suggested that during the Cretaceous there was much evolutionary experimentation among tribosphenic mammals in that the tribosphenic condition may have arisen more than once, and lineages may have evolved within that group which were neither marsupials nor placentals (Clemens & Lillegraven 1986, Marshall & Kielan-Jaworowska 1992, Sigogneau-Russell 1995). The Deltatheroida have been interpreted in this way, being regarded as a sister-group of the Marsupialia (*sensu* Kielan-Jaworowska & Nessov 1988). The Deltatheroida have features suggestive of placentals, such as the placement of the three principal talonid cusps on the lower molars, as well as those character states which associate them with marsupials; e.g. sharp difference in morphology between the most posterior premolar and most anterior molar and dental formula (Kielan-Jaworowska & Nessov 1988). In an analogous fashion, this same region of the molar talonid of *Ausktribosphenos nyktos* resembles that of the marsupials in having a hypoconulid close to the entoconid, and thus *A. nyktos* may prove to be the sister-group of the Placentalia rather than a member of them *sensu stricto*. However, there are undoubted placentals with a similarly placed hypoconulid relative to the entoconid; e.g. UCM 57495, a mandible fragment of the Middle Eocene, North American erinaceid *Entomolestes grangeri* with a complete P_4 and M_1 (fig. 15).

Another possibility championed by Kielan-Jaworowska, Cifelli and Luo (1998, reprinted here in appendix 1) is that *Ausktribosphenos nyktos* is not a member of the Tribosphenida at all. Rather, they regard *A. nyktos* as probably having independently evolved the tribosphenic condition from a symmetrodont ancestor. That such convergent evolution might well have occurred in the Late Jurassic or Early Cretaceous is demonstrated by the existence of the therian *Shuotherium dongi* Chow & Rich (1982) (see also discussion in Wang et al. 1998). On *S. dongi* there is a structure on the lower molars termed the pseudotalonid, which was interpreted as the functional equivalent of the talonid on the Tribosphenida. However, being anterior to the trigonid instead of posterior as in the Tribosphenida, it is inconceivable that the pseudotalonid was derived from the true talonid or, alternatively, gave rise to it. If structures which functioned as talonids arose twice among therian mammals, there is no reason in principle why they could not have been derived more often than that. Marshall and Kielan-Jaworowska (1992), for example, speculate that the tribosphenic condition arose independently in the marsupials and placentals.

That *Ausktribosphenos nyktos* represents yet another example of the independent acquisition of the tribosphenic condition, however, requires invoking the hypothesis that the several features of *A. nyktos* which suggest its affinities with placentals are convergent as well. Although not impossible, the required coincidence of the simultaneous presence of these several different, functionally independent characters, suggests caution in accepting an extraordinary case of convergence as the explanation for the morphology of *A. nyktos* remarkably resembling some members of the Placentalia.

Archer (in Musser & Archer 1998) made this brief comment about the holotype of *Ausktribosphenos nyktos*, '...one of us (M.A.) has seen the specimen and is convinced that this small jaw is not that of a placental mammal but instead may share a relationship with peramurids or possibly with monotremes.' As no evidence was cited for this view and no level of relationship between the groups specified, it is not possible to frame a general response to this comment. The features of *A. nyktos* that separates it from the monotremes are discussed above in the *Diagnosis*, *Molar wear facets*, and *Discussion*. In the case of peramurids, if it is accepted that *A. nyktos* is at least functionally a tribosphenic mammal, it is not a peramurid by any example of previous useage of which the authors are aware.

Kielan-Jaworowska, Cifelli and Luo (1998, reprinted here in appendix 1) made a detailed commentary about the affinities of *Ausktribosphenos nyktos*. A response to this was made by Rich, Flannery and Vickers-Rich (1998, reprinted here in appendix 2).

Infraclass Pantotheria Simpson 1929
Order Eupantotheria Kermack and Mussett 1958
Family Uncertain
Teinolophos gen. nov.

Figure 17. (a) Stereophotographs of mammalian jaw fragment with at least one root in cross-section, MSC 147, [= NMV P208230]. X9.35. (b)–(c). Stereophotographs of the holotype of *Teinolophos trusleri*, MSC 148, [= NMV P208231]. (b) Occlusal view, (c) Lingual view. X8.87.
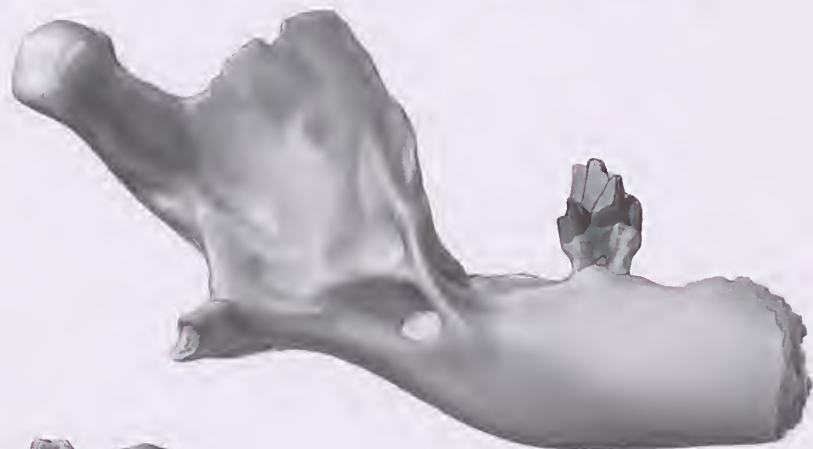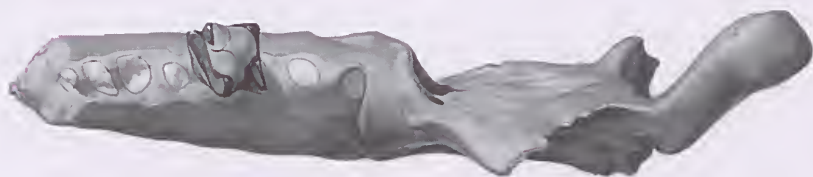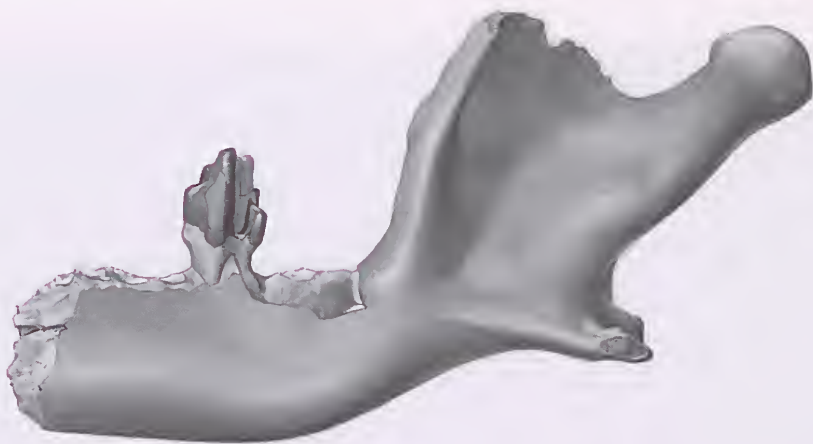
Trusler 1998.

Type species. *Teinolophos trusleri* sp. nov.

Diagnosis. Distinguished from other eupantotheres by the talonid of the penultimate posterior molar being extremely foreshortened and yet extending further labially than the trigonid.

Etymology. *Teino*, Greek, adjective, 'extended', *lophos*, Greek, masculine noun, 'ridge', in reference to the pronounced labial projection of the crest present on the talonid of the penultimate molar.

Teinolophos trusleri sp. nov.

Holotype. MSC 148 [= NMV P208231]. Left mandible fragment significantly crushed with condyle, base of ascending ramus and angular process, and a single, heavily encrusted tooth, the penultimate posterior lower molar (figs 16, 17b, 17c, 18).

Diagnosis. That of the genus until other species are described.

Etymology. Named in honour of Mr Peter Trusler whose artwork has done so much to both accurately portray fossil vertebrate specimens as well as to restore the living animals of which they were once a part, in particular these Mesozoic mammals of Australia.

Description. Although heavily damaged, this jaw fragment has more of the angular process and ascending ramus preserved than any of the material referred to *Ausktribosphenos nyktos.* Also, the condyle is preserved, which is unknown in *A. nyktos.*

The mandibular foramen is much larger than that in *Ausktribosphenos nyktos* and located more anteriorly, lying beneath the anterior edge of the ascending ramus rather than about 40% of the distance from that point to the angular process. Running along the nearly vertical anterior edge of the ascending ramus are two narrow ridges, one of which projects labially and the other, lingually. In contrast, in *A. nyktos,* there is only a labial ridge bounding the anterior edge of the masseteric fossa. Along the base of the masseteric fossa is a horizontal ridge, which terminates posteriorly at the angular process. This ridge is much higher but narrower than that in *A. nyktos.* On the lingual side of the jaw, there is a corresponding horizontal ridge which extends posteriorly from the mandibular foramen again to the base of the angular process. Projecting labially, lingually and posteriorly from the body of the mandible, the angular process forms a nearly horizontal plate that is noticeably wider than that structure in *A. nyktos.* In *A. nyktos,* the angular process projects only posteriorly and labially. The condyle lies

Figure 18 (Opposite). *Teinolophos trusleri,* MSC 148, [= NMV P208231]. (a) Labial view of jaw, x10, (b) Occlusal view of jaw, x10, (c) Lingual view of jaw, x10, (d) Posterior view of jaw, x10, (e) Posterior view of molar, x20.

slightly higher than the top of the one partial molar preserved. A prominent groove parallels the posterior border of the jaw between the mandibular process and the condyle. It is well separated from the mandibular foramen.

The single tooth preserved is the penultimate posterior molar. Owing to the intractable nature of the matrix still clinging to the specimen, particularly in the trigonid area, the tooth is not fully exposed. This makes it difficult to interpret. It has two equal-sized roots. In lingual view, the two are equal in their exposed anteroposterior width but in labial view, the one beneath the trigonid is noticeably larger. There is a prominent precingulid along the base of the prevallid, which displays a prominent wear facet. Based on what can be seen in lingual view, the paraconid is much higher than the metaconid in the posterolingual corner of the tooth. However, the metaconid is broken so its original height is uncertain. Projecting labially and slightly posteriorly from a point somewhat labial to the base of the metaconid is a bladelike ridge, which terminates at a point slightly more labial than the protoconid. This blade is significantly lower than the protoconid, in occlusal view is weakly concave posteriorly, and separated from the trigonid by a deep notch on the labial side of the tooth. No cuspules are preserved on this blade. However, the midsection of the crest of the blade is damaged so a cuspule may have been present. Given the unusual orientation of this blade plus the lack of any indication of a cusp upon it, we hesitate to homologise it with any of the structures known on the talonids of other eupantotheres.

Measurements (in mm) of
penultimate posterior molar of MSC 148

Trigonid length:	1.2
Trigonid width:	1.3

Discussion: As utilised in this paper, the contents of Order Eupantotheria Kermack and Mussett 1958 are taken to be those taxa listed in McKenna and Bell (1997) as being in the Legion Cladotheria McKenna 1975 minus those in the Infralegion Tribosphenida McKenna 1975. While this concept of the Eupantotheria is a paraphyletic group with all the shortcomings pointed out by Prothero (1981), it is still a quite useful shorthand to indicate with which assemblage of higher taxa *Teinolophos trusleri* is to be associated on the basis of current knowledge.

Encrusted though the holotype of *Teinolophos trusleri* still is in critical areas such as the trigonid of the single molar and battered though the mandible is, the presence of a well-defined mandibular angle plus the obvious triangular form of the single known molar strongly indicate that *Teinolophos trusleri* is some kind of eupantothere (Kraus 1979). The talonid, being both extremely foreshortened yet with a single blade on it oriented almost mediolaterally that extends further labially than the base of the protoconid, has a combination of features not even

closely matched among other eupantotheres. Careful examination of the posterior side of the talonid confirms that this unusual configuration for a eupantothere lower molar is not an artifact.

Mammalia

Material: MSC 146 [= NMV P208229]. Uncrushed mandible fragment with one root clearly preserved (fig. 17a).

Description: The cross-section of the one thecodont tooth root preserved in this specimen is bean-shaped rather than circular. On double-rooted mammalian tooth, there is a vertical groove on each of the roots that is located on the side opposite the other root, resulting in each root having a bean-shaped cross-section.

Biogeography

Knowledge of the late Tertiary fossil record of Australian terrestrial mammals has now reached a point sufficient to outline the general pattern of their history during that time interval (Rich 1991). Among the generalisations that can be made from it, two are relevant here. First, by the beginning of the late Tertiary there were no terrestrial placental mammals in Australia. Second, about the beginning of the Pliocene, murid rodents entered Australia via dispersal by island hopping from south eastern Asia. The only other terrestrial placentals to subsequently reach Australia were humans and the species they brought with them. The fossil record also shows that by the end of the Early Cretaceous, monotremes were present in Australia, and marsupials are known in the oldest Cainozoic land mammal faunas yet found on the continent (Rich 1991).

The evidence relating to the history of terrestrial mammals within Australia accorded well with the general picture of the global history of the group that was supported by all available evidence and generally accepted prior to 8 March 1997. In that view, placentals appeared in Asia by the end of the Early Cretaceous, marsupials evolved in North America with their oldest record being slightly younger, early Late Cretaceous, and monotremes had evolved in Australia by the late Early Cretaceous (fig. 19a) (Marshall & Kielan-Jaworowska 1992; Rich 1991). Well before the end of the Cretaceous, placentals had reached North America. Subsequently, at about the Cretaceous–Tertiary boundary, marsupials and placentals entered South America where they encountered monotremes which had probably crossed Antarctica from Australia, if they did not originate there (Pascual, Jaureguizar & Prado 1996). Both marsupials and placentals continued southward to reach the Antarctic Peninsula by the Eocene (Marenssi et al. 1994), but from there, only the marsupials reached Australia (fig. 19b)[1].

In the late Cainozoic, marsupials, which had earlier spread to all the continents, became restricted to the Americas and Australia. Monotremes disappeared from South America, and, except for marine placentals, all three groups became extinct on the Antarctic continent (fig. 19c).

Rainger (1991) traces the idea that marsupials and placentals originated in the northern hemisphere and spread to the southern, from Charles Darwin and Alfred Russel Wallace in the latter half of the 19th century. This concept was then further developed in the early 20th century by William Diller Matthew and subsequently championed by George Gaylord Simpson who both, like Wallace, utilised the mammalian fossil record to support their interpretations.

Although not a single fossil specimen of an Australian mammal has been found in rocks younger than Early Cretaceous and older than Eocene (a gap of more than 50 million years), the view that marsupials did not reach the continent until around the Cretaceous–Tertiary boundary was widely accepted because of what was known about the Late Cretaceous mammalian fauna of South America and the evident linking at that time of the two continents via East and West Antarctica.

The single most critical piece of evidence was the nature of the Campanian (late Late Cretaceous) Los Alamitos fauna from northern Patagonia, Argentina. This fauna came to light in the 1980s owing to the efforts of José Bonaparte and his colleagues. What they found was a diverse mammalian fauna that completely lacked evidence of both marsupials and placentals. Rather, it was a mixture of endemic forms unknown in the northern hemisphere, together with archaic mammals that were more typical of the Jurassic than the Cretaceous elsewhere (Bonaparte 1990).

Bonaparte concluded that not only South America, but the Gondwana continents as a whole, had lacked both marsupials and placentals until about the Cretaceous–Tertiary boundary when there was a link between North America and South America (Bonaparte 1990, 1994). He further pointed out that the dinosaurs of South America were quite unlike those of the northern continents until the last stage of the Cretaceous, the Maastrichtian. This, too, was seen as part of a broader isolation of the Gondwana continents from those of Laurasia in the Cretaceous.

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[1] The holotype of *Tingamarra porterorum* is a right lower molar identified as Infraclass Placentalia, Order ? Condylarthra from deposits in south-eastern Queensland reported as Early Eocene in age (Godthelp et al. 1992). Identification of this specimen as a placental has been questioned by Szalay (1994) and also by Woodburne and Case (1996), who also expressed doubts that the age of the site is as old as Eocene.

Middle Cretaceous — Pre 8 March 1997
120–80 Million Years Before Present

Early Cainozoic
60–40 Million Years Before Present

Late Cainozoic
20 Million Years Before Present – Present
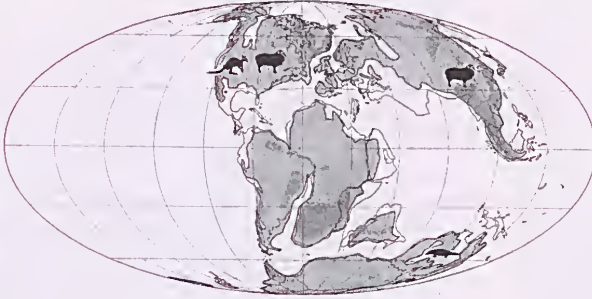
Figure 19. Three maps showing the distribution of three major mammalian groups during the Cretaceous and Cainozoic as interpreted from fossil data prior to 8 March 1997.
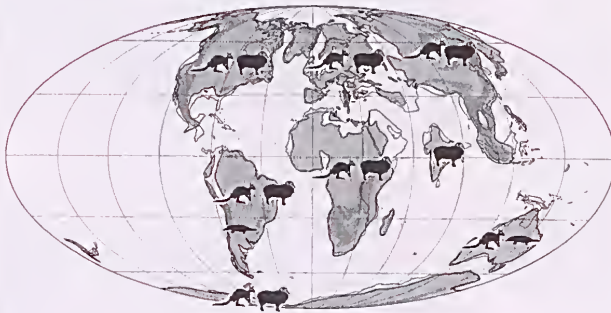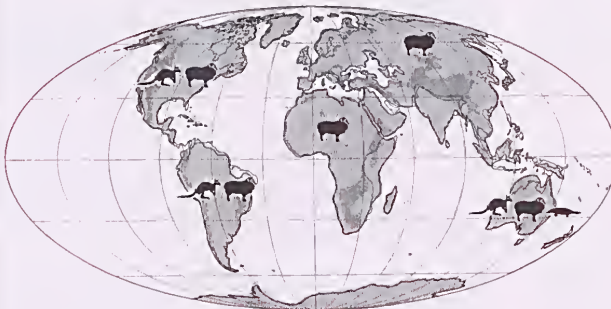
Placental:

Marsupial:

Monotreme:

(a) In the Cretaceous Period, monotremes existed in Australia and placentals and marsupials were restricted to the northern hemisphere. Palaeogeographic map of land surfaces during the Aptian (late Early Cretaceous) 115 million years ago. Mollweide projection (Smith, Smith, & Funnell 1994).

(b) In the early Cainozoic Era, monotremes reached South America and Antarctica from Australia and marsupials and placentals reached those continents from North America. From Antarctica, marsupials but not placentals reached Australia. Placentals also reached Europe and Africa, while marsupials reached those continents plus Asia. Palaeogeographic map of land surfaces during the Early Eocene, 53 million years ago. Mollweide projection (Smith, Smith, & Funnell 1994).

(c) By the late Cainozoic Era, all terrestrial mammals became extinct in Antarctica. Marsupials became extinct in Asia, Africa, and Europe. Terrestrial placentals reached Australia by the Pliocene, while bats preceded them, probably in the early Cainozoic. Palaeogeographic map of land surfaces during the Pliocene, 5 million years ago. Mollweide projection (Smith, Smith, & Funnell 1994).

Paths of Interchange

If *Ausktribosphenos nyktos* is a placental, after its common ancestor with *Prokennalestes* divided, the possible routes for the descendants of that common ancestor to pass between Australia and Asia are significantly constrained by the time of separation of those continents. That phyletic event probably happened during the first 20–25 million years of the 49 million year time span of the Early Cretaceous, that is, prior to when those two genera lived. This is because with one possible exception, there is no evidence for the existence of tribosphenic mammals prior to the Cretaceous. An unnamed, isolated molar talonid from the Berriasian (earliest Early Cretaceous) of England is considered to be the oldest tribosphenic mammal known at present (Sigogneau-Russell & Ensom 1994). The possible exception is a single isolated upper molar of what may be a tribosphenic tooth from the Late Jurassic of China (Wang et al. 1998). However, this tooth is probably an upper molar of *Shuotherium* and hence, pseudotribosphenic rather than tribosphenic (Chow & Rich 1982).

Reconstructions of continental positions during the Early Cretaceous (e.g. fig. 20) suggest that the most likely route between Australia and Asia would have been a roundabout one via Antarctica, then to South America, Africa, Europe and finally to Asia. As mentioned above, in the mid-1980s Bonaparte first hypothesised that all of Gondwana lacked tribosphenic mammals including placentals until the end of the Cretaceous, and that its dinosaurs at the time were endemic until the last stage of that period. This has been challenged in the case of Africa during the Early Cretaceous, e.g. Sigogneau-Russell (1995) for mammals, Sereno et al. (1996) for dinosaurs. However, his view still holds for South America, e.g. (Bonaparte 1994) for mammals and (Novas 1997) for dinosaurs.

Given the position of continents during the Early Cretaceous and the quality of the fossil record in various regions, the most likely case is that placentals did reach South America at that time and subsequently became extinct, as they appear to have done in Australia and certainly did in Antarctica. Bonaparte (1994) suggested much the same thing when he wrote the following.

'It is not improbable that the eventually unsuccessful evolution of pre-tribosphenic mammals of South America as *Vincelestes* (BONAPARTE and ROUGIER, 1987), fig. 7, from the late Neocomian (Hauterivian), or tribosphenic mammals of Africa as *Tribotherium* (SIGOGNEAU-RUSSELL, 1991) from the Neocomian, is the result of the variety of adaptive types developed by the Dryolestida, which may have been dominant in the evolutionary scenario of Cretaceous mammals of South America and eventually of Africa.'

Another possibility is that placentals did persist in South America during the Late Cretaceous after having arrived there in the Early Cretaceous. This would require that for some reason they have not been recovered from the abundant Los Alamitos fauna.

It is conceivable that South America was not part of the pathway for placental interchange between Australia and Asia. It could be that Africa served as the sole link between Antarctica and the Laurasian continents. In that case, placentals simply did not reach South America until much later. However, if that were true, it is difficult to understand why, as Africa and South America were still broadly linked during the Early Cretaceous. Furthermore, at that time, Africa was well separated from Antarctica by a broad seaway, whereas South America was much closer.

Detailed reconstructions of the plate tectonic history of China and South-east Asia presented in Metcalfe (1996) offer another possibility for a direct route of interchange between Australia and Asia. China and South-East Asia were formed by the fusion of a series of micro-continental plates, or terranes, which had their origin in the part of Eastern Gondwana to the north and north-west of Australia. During the Phanerozoic, successive terranes broke away from Eastern Gondwana and moved northward to eventually collide with and accrete to south-eastern Asia. Figure 20 (figure 16 in Metcalfe 1996) shows the Late Jurassic – Late Cretaceous phase of this process.

Plate tectonic reconstructions of the entire Earth for any stage during the Early Cretaceous, such as that in figure 21, commonly imply that there was nothing but open ocean between Australia and south-eastern Asia, a gap half again as great as the shortest distance between modern day South America and Africa. By contrast, the reconstruction in Metcalfe (1996) (fig. 20) that focuses on this area, shows several probable islands in that Late Mesozoic ocean that now form part of the South-East Asian land mass. While these islands may have existed, it is unlikely that island hopping during the Early Cretaceous would have been sufficient by itself to enable interchange of terrestrial mammals between Australia and Asia via that route. If Cretaceous island hopping were feasible, it is difficult to understand why the reasonably well known early Late Tertiary terrestrial mammalian faunas of Asia and Australia are so extremely different, not sharing a single family in common (Rich 1991, Savage & Russell 1983). Presumably such an island hopping route would have become progressively easier for terrestrial mammals to traverse as Australia approached Asia during the Cainozoic.

However, there is still another possibility that might be invoked: a combination of island hopping and McKenna's Noah's Arks (McKenna 1973). Examination of figure 20 shows that individual land masses required about 80 million years to make the transit from Eastern Gondwana to the Eurasian land mass. For example, in the Late Jurassic, the West Burma microplate shown in figure 20
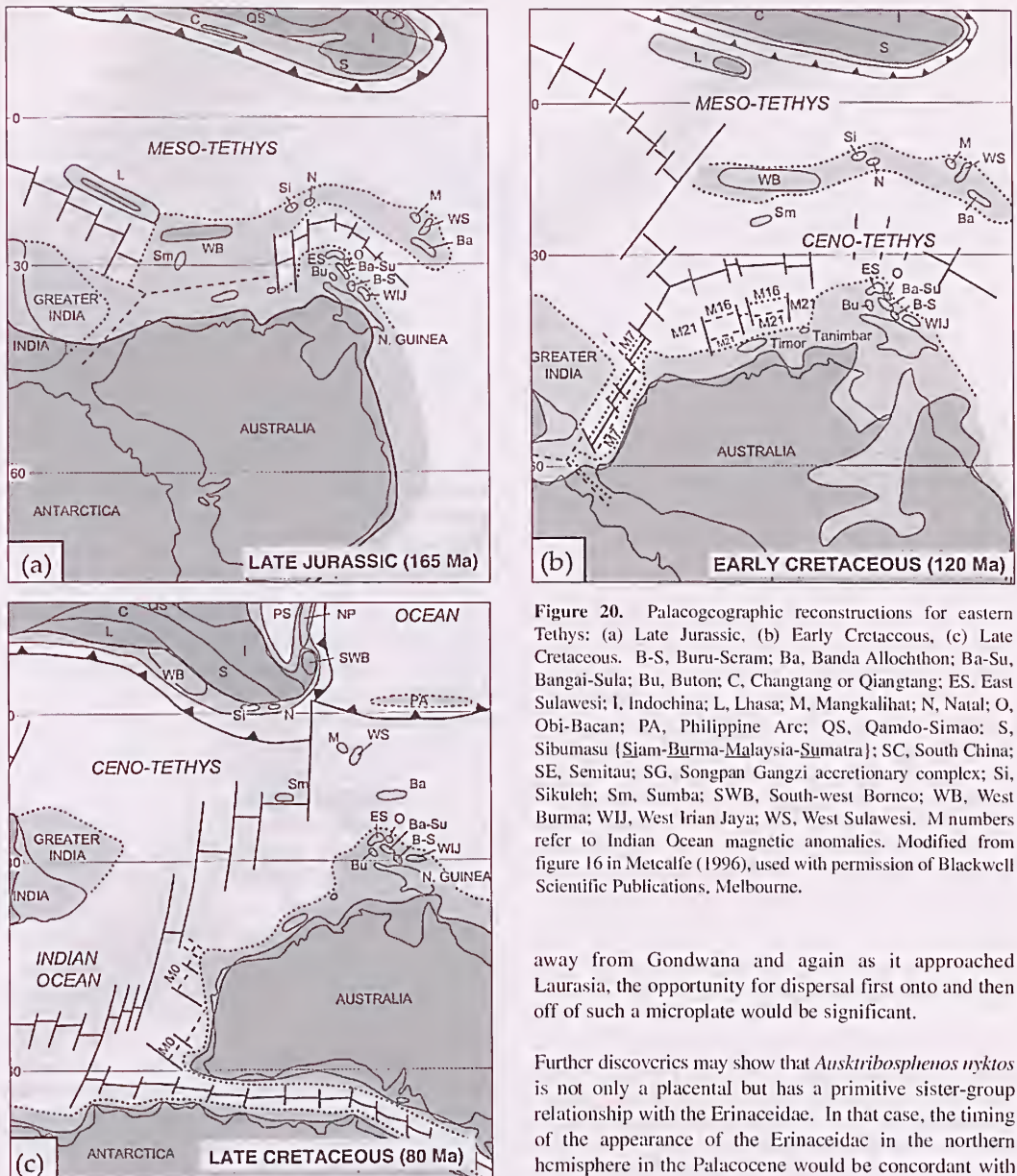
Figure 20. Palaeogeographic reconstructions for eastern Tethys: (a) Late Jurassic, (b) Early Cretaceous, (c) Late Cretaceous. B-S, Buru-Seram; Ba, Banda Allochthon; Ba-Su, Bangai-Sula; Bu, Buton; C, Changtang or Qiangtang; ES, East Sulawesi; I, Indochina; L, Lhasa; M, Mangkalihat; N, Natal; O, Obi-Bacan; PA, Philippine Arc; QS, Qamdo-Simao; S, Sibumasu {Siam-Burma-Malaysia-Sumatra}; SC, South China; SE, Semitau; SG, Songpan Gangzi accretionary complex; Si, Sikuleh; Sm, Sumba; SWB, South-west Borneo; WB, West Burma; WIJ, West Irian Jaya; WS, West Sulawesi. M numbers refer to Indian Ocean magnetic anomalies. Modified from figure 16 in Metcalfe (1996), used with permission of Blackwell Scientific Publications, Melbourne.

away from Gondwana and again as it approached Laurasia, the opportunity for dispersal first onto and then off of such a microplate would be significant.
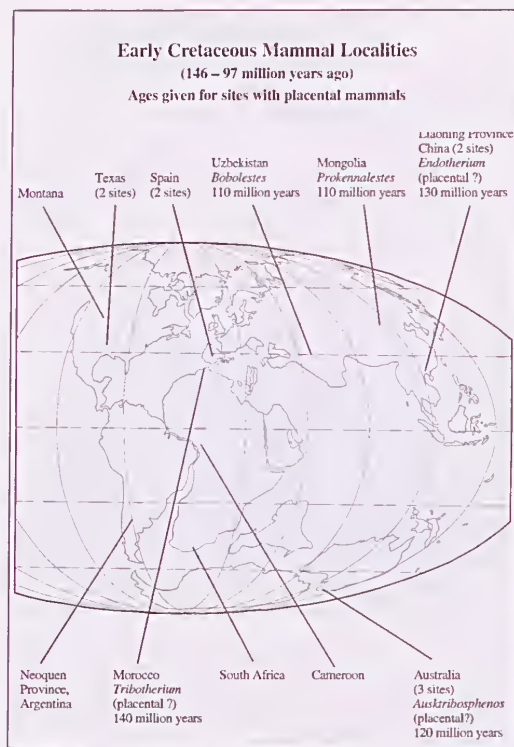
Further discoveries may show that *Ausktribosphenos nyktos* is not only a placental but has a primitive sister-group relationship with the Erinaceidae. In that case, the timing of the appearance of the Erinaceidae in the northern hemisphere in the Palaeocene would be concordant with this mechanism of dispersal.

Such a route might also explain other distributional anomalies. South America does not have records of any of the following dinosaurs prior to the Maastrichtian (latest Late Cretaceous) if at all: ornithomimosaurs, oviraptorosaurs, protoceratopsians, and ankylosaurs (Novas 1997). It is thought those dinosaur groups in this list that did reach South America did so as part of a general episode of interchange with North America in the Maastrichtian. In contrast, these four groups are all well known in Asia by the early Late Cretaceous (Barsbold 1997, Dong 1997) and records of each, admittedly for the

is reconstructed as part of the East Gondwana landmass. At the end of the Cretaceous, it was part of the Eurasian land mass. Hence, the West Burma microplate may have carried a component of the Gondwana biota to Eurasia in its transit; i.e. it acted as a Noah's Ark *sensu* McKenna (1973).

If 80 million years were required for such a northward transit from Eastern Gondwana to Eurasia, it would appear to be too slow to explain the movement of placentals from Australia to Asia in the first half of the Early Cretaceous. However, as a microplate first broke

Early Cretaceous Mammal Localities
(146 – 97 million years ago)
Ages given for sites with placental mammals

Montana

Texas
(2 sites)

Spain
(2 sites)

Uzbekistan
Bobolestes
110 million years

Mongolia
Prokennalestes
110 million years

Liaoning Province
China (2 sites)
Endotherium
(placental ?)
130 million years

Neoquen
Province,
Argentina

Morocco
Tribotherium
(placental ?)
140 million years

South Africa

Cameroon

Australia
(3 sites)
Ausktribosphenos
(placental?)
120 million years

Figure 21. Areas where Early Cretaceous mammals are known. Paleogeographic map of land surfaces during the Aptian, late Early Cretaceous, 115 million years ago. Mollweide projection (Smith, Smith & Funnell 1994).

most part being based on a single or a few bones, occur in the late Early Cretaceous of Australia (Currie, Rich & Vickers-Rich 1996, Molnar 1980, Rich & Vickers-Rich 1994).

Biogeographic Conclusions

If the Ausktribosphenidae should prove not to be placental mammals, then the widely received view that the placentals first evolved in Laurasia and dispersed to the Gondwana continents about the time of the Cretaceous–Tertiary boundary is unchallenged by these fossils.

However, given that there were one or more placental mammals in the late Early Cretaceous of Australia as well as in Asia, there appear to be five possible explanations as to how this occurred. In the first, second, and third hypotheses, the roundabout pathway via Antarctica – South America – Africa – Europe was followed. In the first of those, placentals followed this route in the Early Cretaceous only to have become extinct on at least South America by the end of the Late Cretaceous. If the ausktribosphenids are placentals, such an extinction of terrestrial placentals did take place in Australia by the beginning of the late Tertiary. Also, terrestrial placentals became extinct in Antarctica sometime between the Eocene and

the Holocene. So, an extinction of placentals in South America by the Late Cretaceous would not be unprecedented.
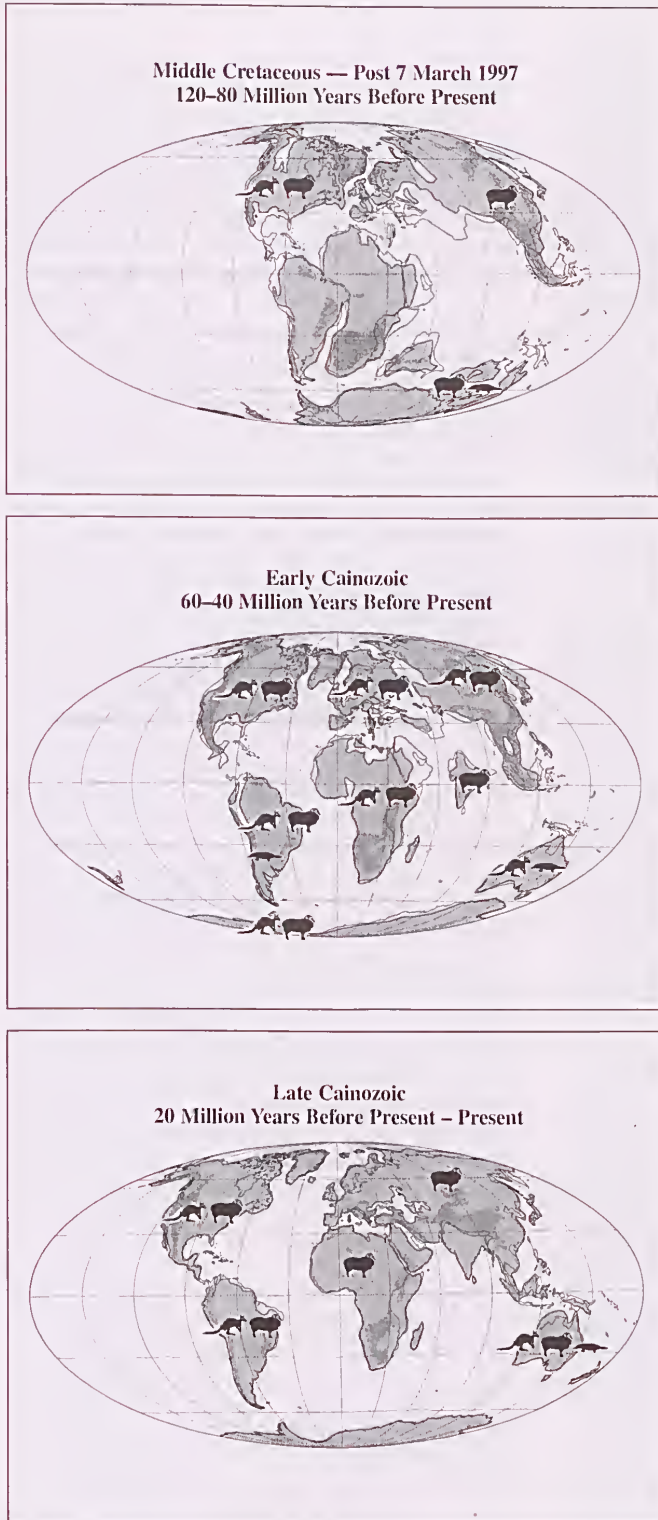
The second hypothesis explains the absence of placentals from the Late Cretaceous of South America as owing simply to the incompleteness of the fossil record, the Campanian Los Alamitos Fauna being highly anomalous in its lack of any tribosphenic mammals, much less placentals.

The third is that the route bypassed South America altogether, using the seemingly less direct connection between Africa and Antarctica.

The fourth and fifth hypotheses are based on a more direct link between Asia and Australia. In the fourth, some of the terranes that are now a part of South-east Asia acted as island stepping stones for placental mammals dispersing between the two continental areas by island hopping. The fifth hypothesis invokes island hopping together with a significant northward movement towards Asia of the placentals on terranes that are now part of South-east Asia. Because this route was evidently not utilised in the Cainozoic until the Pliocene, and the rate of northward movement of continental microplates was so slow at this time, this more direct link is judged to be less likely than the roundabout one to have been the route of interchange in the Early Cretaceous.

Of the five biogeographic hypotheses proposed on the assumption that there were placentals in the Early Cretaceous of Australia, the first, which invokes the extinction and subsequent reintroduction of placentals in at least South America and Australia, if not all of Gondwana, seems to us to be the least contrived for the data currently available. If not the first hypothesis, at least the roundabout route between Asia and Australia seems more plausible than the direct one. If that is the case, with one modification, the addition of a single icon representing placentals in Australia in figure 19, the most parsimonious interpretation of the sequence of distribution maps (figs 22a-c) is quite different. Instead of the placentals having originated in Asia by the Early Cretaceous and dispersing from there, the known occurrence of placentals in the Early Cretaceous in two areas of the world nearly as far apart as they could possibly have been at that time supports the hypothesis that these mammals were then widespread, and no single area can be picked out at present as that most likely to be the one where they arose. This accords well with the view of Lillegraven et al. (1987), who suggested that the split between the marsupials and placentals could have taken place anywhere, '...on the earth's dry surface.'

The presence of *Teinolophos trusleri* in the Early Cretaceous of Australia is fully in accordance with the hypothesis of Bonaparte (1990) that during that time, the Gondwana continents as a whole were host to archaic mammals including eupantotheres.

Middle Cretaceous — Post 7 March 1997
120–80 Million Years Before Present

Early Cainozoic
60–40 Million Years Before Present

Late Cainozoic
20 Million Years Before Present – Present

Figure 22. As a consequence of the discovery of the possible placental *Ausktribosphenos nyktos*, the series of events portrayed in figures 19a-c takes on quite a different interpretation. This series of maps differs from those in figure. 19 solely in that in the Cretaceous Period, placentals are added to the Australian map (fig. 22a). In light of this one addition, instead of seeing placentals dispersing from the northern hemisphere to the southern hemisphere in the latest Cretaceous and/or early Tertiary, it is just as likely that they were widespread over the globe by the end of the Early Cretaceous and what is seen in figure 22b reflects not so much dispersal as previously thought, but simply improvement in the quality of the mammalian fossil record during the early Cainozoic. Palaeogeographic map of land surfaces during the Aptian, late Early Cretaceous, 115 million years ago (fig. 22a), Early Eocene, 53 million years ago (fig. 22b), and Pliocene, 5 million years ago (fig. 22c). Mollweide projection (Smith, Smith & Funnell 1994).

Conclusions

Just over a century ago, the geologist Thomas Crowder Chamberlin (1890) wrote a paper on the strategy of scientific investigation entitled, 'The Method of Multiple Working Hypotheses. With this method the dangers of potential affection for a favorite theory can be circumvented.' The subtitle offers a warning that is particularly relevant in cases such as the analysis of the fossils described here where there is a paucity of evidence. Hence, the authors made a deliberate attempt to test as many hypotheses as feasible and to present all that came to mind which could not be rejected.

This does not mean that all hypotheses put forward by us have equal plausibility in our minds. At this stage of our knowledge, it seems more likely to us that *Ausktribosphenos nyktos* is a placental mammal rather than a sister-group of the Placentalia or a member of a lineage which acquired the tribosphenic condition of its lower molars independent of all members of the Tribosphenida. However, those latter two hypotheses cannot be rejected at present.

Of the five biogeographic hypotheses presented, at this time one seems most likely to us. It is that from the common ancestor of *Prokennalestes* in Mongolia and *Ausktribosphenos* in Australia, the route of migration linking these two known genera passed via Antarctica, South America, Africa, and Europe. Under this hypothesis, it is most likely that the placentals became extinct in South America by the Campanian, the age of the Los Alamitos fauna, which lacks tribosphenic mammals. However, if the features suggestive of a close relationship between *Ausktribosphenos nyktos* and the Erinaceidae should prove, with further knowledge, to be phylogenetically significant, rather than an incredible case of convergence, then the hypothesis of a one-way dispersal route from Eastern Gondwana to South-East Asia via a Noah's Ark mechanism would become a significantly more persuasive hypothesis.

Finally, in framing any biogeographic hypothesis concerning mammalian distribution, it is well to keep in mind the comparative lack of information available concerning the distribution of mammals during the Early Cretaceous (fig. 21). Nearly 50 million years in duration, it is 80% the length of the Cainozoic Era. Yet the quantity of terrestrial mammalian fossils from the Early Cretaceous now in museums would be no more than a few kilogrammes, whereas the Cainozoic record would be measured in hundreds, if not thousands of tonnes. Crude though such a rough estimate of the comparative weight of the available fossil specimens admittedly is, it does accurately convey the point that the Cainozoic material record of terrestrial mammals is somewhere in the vicinity of five to eight orders of magnitude greater than that which is available for the Early Cretaceous.

The presence of *Teinolophos trusleri*, a mammal from the Flat Rocks site that is clearly not *Ausktribosphenos nyktos*, suggests that further excavation at that locality can reasonably be expected to yield a diversity of mammals.

Acknowledgements

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Alleged Cretaceous placental from down under

ZOFIA KIELAN-JAWOROWSKA, RICHARD L. CIFELLI AND ZHEXI LUO

The significant discovery of a dentary with four teeth of *Ausktribosphenos nyktos* from the Early Cretaceous of Australia by Rich *et al.* (1997) raises fundamental issues regarding mammalian evolution and paleobiogeography during the Mesozoic. The authors recognized the three last molariform teeth as molars and the preceding tooth as a premolar, and on this basis suggested that *A. nyktos* is a placental. Rougier & Novacek (1998) briefly criticized this idea in a popular review. Here we offer the interpretation that this extraordinary fossil has its affinities among extremely primitive mammals – early symmetrodonts – rather than placentals.

Ausktribosphenos nyktos lacks several diagnostic mandibular features of placentals, marsupials, and their relatives, such as 'eupantotheres' and advanced symmetrodonts. In *A. nyktos* (Fig. 1), the mandibular foramen is located in contact with the Meckel's groove, as in primitive mammals such as *Kuehneotherium* (Kermack *et al.* 1968) and the docodont *Haldanodon* (Lillegraven & Krusat 1991), whereas the foramen and groove are well separated in advanced symmetrodonts and 'eupantotheres' (Prothero 1981), as well as in therians (Kielan-Jaworowska 1981; Kielan-Jaworowska & Dashzeveg 1989). Moreover, at the posterior part of the dentary in *A. nyktos* is a broad trough with scars for several bones, as in primitive mammals such as *Kuehneotherium* but unlike the therian condition. The presence of the trough suggests that the postdentary bones were probably attached to the dentary, quite different from the homologous middle ear bones of extant mammals and extinct multituberculates (Rougier *et al.* 1996).

A. nyktos does not possess the angular process for the insertion of the masseter superficialis (Gambaryan & Kielan-Jaworowska 1995), as in extinct 'eupantotheres', marsupials, and early placentals (Prothero 1981; Kielan-Jaworowska & Dashzeveg 1989), indicating that its masticatory musculature differed from that of living therians. The posterior part of the dentary in *A. nyktos* most resembles those of the archaic symmetrodont *Kuehneotherium* (Kermack *et al.* 1968) and aberrant *Shuotherium* (Chow & Rich 1982). A hypothetical relationship of *A. nyktos* to placentals would thus require independent changes of these postdentary bones and mandibular features. Based on the mandibular characters, we suggest that *A. nyktos* represents a relict of a more ancient radiation, possibly originating from primitive symmetrodonts, known from a well-established fossil record on the Gondwana continents (Bonaparte 1990; Sigogneau-Russell 1991).

Evidence from the dentition is equivocal. The last premolar (which resembles a symmetrodont molar) has a trigonid but no talonid, unlike any early placental (e.g., Kielan-Jaworowska & Dashzeveg 1989; Kielan-Jaworowska 1981). The molars, with extensive labial cingulum and short talonid, also differ significantly from those in known tribosphenic mammals. Wear facets (see Crompton 1971 for terminology of facets and interpretation), cited as showing a diagnostically tribosphenic pattern, are also equivocal. In particular, facet 5 (indicating presence of a protocone or similar structure) is indistinct from the primitively present facet 1, the orientation and placement of facets 6 are unlike the condition in primitive tribosphenic mammals, and facet 4 (indicating the presence of a metacone, present in tribosphenic mammals and their relatives) is lacking.
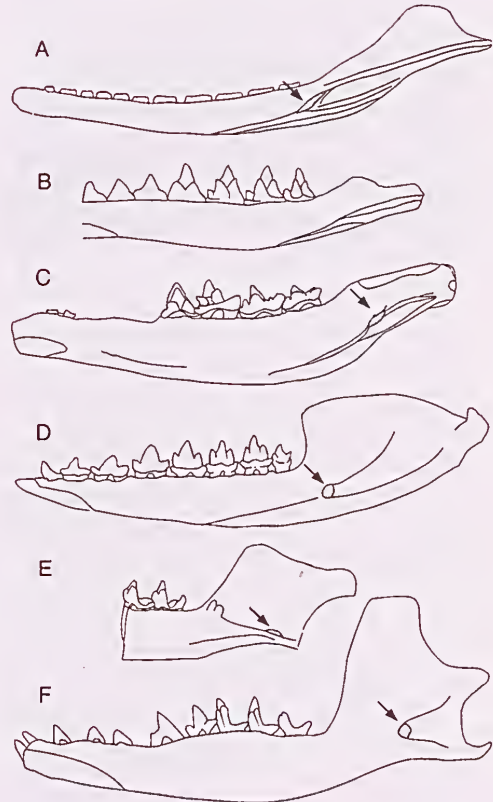

Fig. 1. Right dentaries rendered to approximately the same length, medial views. □A. Primitive symmetrodont *Kuehneotherium*. □B. Aberrant symmetrodont *Shuotherium*. □C. *Ausktribosphenos*. □D. Advanced symmetrodont *Tinodon*. □E. Early Cretaceous placental *Prokennalestes*. □F. Late Cretaceous placental *Asioryctes*. The arrows denote the mandibular foramen situated in contact with the Meckel's groove in A and C, and separated from it in D–F (unknown in B). Note angular process in E (broken) and F, absent from other dentaries. Modified from: A – Kermack *et al.* (1968); B – Chow & Rich (1982); C – Rich *et al.* (1997); D – Prothero (1981); E – Kielan-Jaworowska & Dashzeveg (1989); F – Kielan-Jaworowska (1981).

The real significance of *A. nyktos*, in our opinion, is that it appears to have independently acquired dental features functionally analogous to those of tribosphenic mammals.

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Alleged Cretaceous placental from down under: Reply

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When Rich *et al.* (1997) named and described the Australian Early Cretaceous mammal *Ausktribosphenos nyktos*, they presented three hypotheses as to its affinities. Their favored hypothesis was that it was a placental mammal. Kielan-Jaworowska *et al.* (1998) countered with the suggestion that *A. nyktos*, 'has its affinities among extremely primitive mammals – early symmetrodonts – rather than placentals'.

In giving their reasons why *Ausktribosphenos nyktos* might be a placental, Rich *et al.* (1997) based their position on more than the dental formula. Their argument for placental affinities of *A. nyktos* was divided into two parts. First, they noted that *A. nyktos* was a tribosphenic mammal. Second, among the tribosphenic mammals, they suggested it was most similar to placentals. The evidence from the dental formula was just one of three criteria supporting the second part of the argument, namely to make an explicit distinction between *A. nyktos* and marsupials. The other two characters distinguishing *A. nyktos* from the marsupials were the lack of an inflected angle (Sanchez-Villagra & Smith 1997) and the submolariform nature of the P_5.

In April, 1998, a second mandible of a mammal, MSC 145 (MSC, Monash Science Centre) (= NMV P208228 [NMV P, Museum Victoria Palaeontological collection]), was found at the holotype locality of *Ausktribosphenos nyktos*. While possibly not *A. nyktos*, it has features of the P_5 talonid and the molar talonids, which clearly place it in the Ausktribosphenidae. This specimen adds relevant information concerning several of the points raised by Kielan-Jaworowska *et al.* (1998).

Prokennalestes trofimovi and *Prokennalestes minor* Kielan-Jaworowska & Dashzeveg 1989 from the Early Cretaceous of Mongolia are species whose placental affinities have never been questioned (e.g., Butler 1990; Cifelli 1993). Like *Ausktribosphenos nyktos*, they too have some primitive features not seen elsewhere in placentals, such as a Meckelian groove and a facet on the dentary for a coronoid bone. These features are not considered sufficient to bar the two species of *Prokennalestes* from the Placentalia. The species of *Prokennalestes* were regarded as placentals principally because of their dental formula and the 'gradual morphological change between the premolars and molars, as is characteristic of the Eutheria'. In these two features, *A. nyktos* agrees with *P. trofimovi* and *P. minor*.

The mandibular foramen on MSC 145 faces posteriorly and is not located in a groove of any kind. Unlike the holotype of *Ausktribosphenos nyktos*, there is no positive trace of a Meckel's groove on MSC 145. However, the preservation of MSC 145 in the area where it would be expected is not good enough to rule out the possibility that there may have been an extremely weak one. Furthermore, in the holotype of *Ausktribosphenos nyktos*, the posteriorly facing mandibular foramen is not located within the Meckelian groove but at the posterior end of it and slightly above. The mandibular foramen and the groove that may have held post-dentary bones (=surangular facet) are separated by a well-developed, although quite narrow, diagonal ridge in the holotype of *A. nyktos*, whereas in MSC 145 the two are much wider apart (compare Fig. 1D and

E). The location of the mandibular foramen with respect to both the Meckelian groove and the more prominent groove behind and below it, which may have held postdentary bones, thus appears to be a variable feature within the ausktribosphenids. But in neither case can the mandibular foramen be characterized as lying within the Meckelian groove.

While there are depressions at the rear of the jaw on both the holotype of *Ausktribosphenos nyktos* and MSC 145, they are quite shallow, as is the case in symmetrodonts. In symmetrodonts, such grooves appear to be vestigial remnants of depressions where post-dentary bones occurred in more primitive mammals and synapsids. In *Morganucodon*, where post-dentary bones do occur, such grooves, are markedly deeper (Kermack *et al.* 1973).

MSC 145 has a well-developed angular process. When this fact became known, the holotype of *A. nyktos* was re-examined at the suggestion of Zofia Kielan-Jaworowska, and a tiny remnant of the anteriormost part of the base of the angular process was found to be present on that specimen as well (Fig. 1D). Therefore, the comments by both Rich *et al.* (1997) and Kielan-Jaworowska *et al.* (1998) about the significance of the supposed absence of the angular process on *A. nyktos* are no longer relevant. What the condition of the angular process in MSC 145 does is to strengthen the case that ausktribosphenids are placentals. In the synapsid *Diarthrognathus*, the primitive mammal or advanced synapsid *Morganucodon*, and the placental *Prokennalestes*, the base of the angular process is quite anterior to the condyle (Fig. 1A–C). On the other hand, in the ausktribosphenids and in more advanced placentals, such as *Asioryctes*, the base of the angular process is typically almost directly below the condyle (Fig. 1D-F). Thus, in this feature the ausktribosphenids are more like the majority of placentals than the unquestioned placental *Prokennalestes*.

Other features of the species of *Prokennalestes* that are more plesiomorphic than in *Ausktribosphenos nyktos* are (1) the P_5 is not as strongly submolariform, (2) the labial masseteric foramen is retained, (3) the talonid basin is narrower, (4) the molar trigonids are higher, particularly the protoconid markedly higher than the metaconid, and (5) the M_3 is subequal in size to the M_1 and M_2, rather than markedly smaller.

While the P_5 of *Ausktribosphenos nyktos* may resemble a symmetrodont molar, it also bears a strong resemblance to the most posterior premolar of some erinaceids, such as *Untermannerix copiosus* Rich 1981. In the case of symmetrodonts with similar molars, there is not just a single molar with a morphology reminiscent of the P_5 of *A. nyktos*, but rather a series of them. In contrast, in erinaceids with a final premolar similar in structure to the P_5 of *A. nyktos*, there is only a single tooth in each jaw with such a morphology. The premolars in front and the molars behind are noticeably different, just as they are in *A. nyktos*.

There may well be no molars of tribosphenic mammals other than those of *Ausktribosphenos nyktos* known with both extensive labial cingulae and short talonids. However, as there is no causal explanation offered why these two features should not occur together in tribosphenic
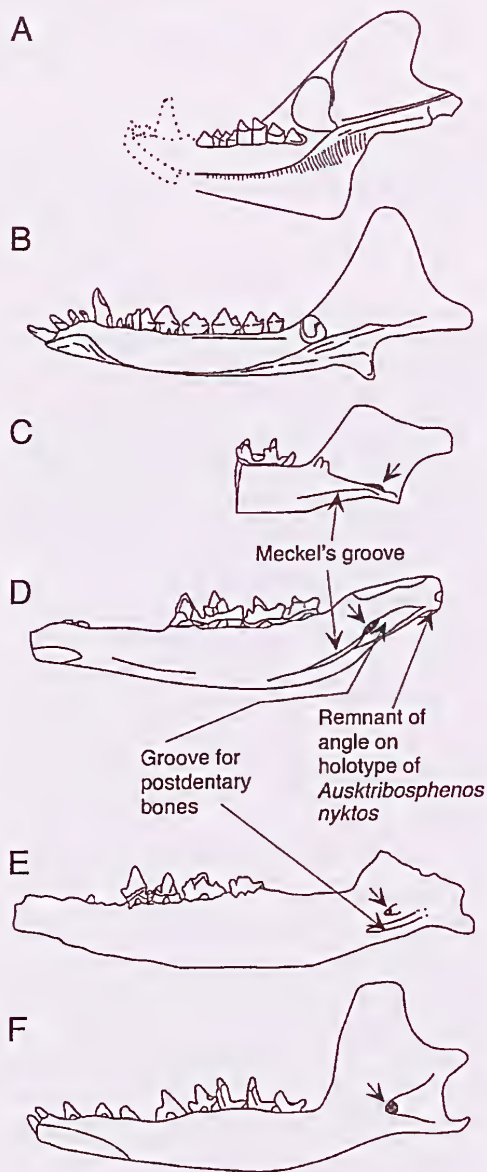
A

B

C

Meckel's groove

D

Groove for postdentary bones

Remnant of angle on holotype of *Ausktribosphenos nyktos*

E

F

mammals, their joint presence in *A. nyktos* is hardly an objection to its being a tribosphenic mammal. Certainly, neither the degree of shortness of the talonid nor the extensiveness of the labial cingulae appear to be unusually striking.

As tribosphenic molars wear, the size and distinctiveness of the various wear facets change. In recognition of this reality, Crompton (1971) remarked how fortunate it was that the specimen of *Didelphodus* sp. he analyzed was at an ideal stage for delimiting the wear facets. While molar wear facet 5 (in the terminology of Crompton 1971) may not be distinct from wear facet 1 in the holotype of *Ausktribosphenos nyktos*, certainly the areas where these two facets are shown to occur in Fig. 3 of Rich *et al.* (1997) are where they would be expected if they coalesced in the course of wear by the upper molars. That such coalescence may have occurred does not suggest that the protocone was absent, merely that a stage had been reached in the wear of the tooth where the boundary has broken down. As wear progresses in a tribosphenic molar, the area of the talonid basin that shows signs of wear increases in size until, typically, the talonid is almost a flat surface. As that happens, the area of wear facet 6 increases. Thus, the area shown as occupied by wear facet 6 in *A. nyktos* is not unusual in its extent. Given the extent of wear facets 1, 5 and 6, the absence of wear facet 4 on the holotype of *A. nyktos* is puzzling. However, if it were present as a small wear facet on the M_{1-2} of the holotype, it could have been present in the damaged parts of those teeth. The facet is also missing on the M_3, and that tooth is undamaged. It is worth noting that on the more heavily worn molars of MSC 145, the area of the talonid where wear facet 4 would be expected is well worn, but it is not delimited as a distinct facet from the wear seen on the rest of the talonid.

If ausktribosphenids are not placental mammals, and for that matter no more advanced than *Prokennalestes*, then they are convergent on them in the development of a talonid basin on their molars, the presence of five premolars and three molars, the submolariform condition of P_5, relatively low molar trigonids, a marked decrease in size posteriorly of the lower molars, the posterior position of the mandibular angle, and the complete loss of the labial mandibular foramen. These features do not form part of any obvious, single functional–adaptive complex. Rather they seem to represent pervasive similarities across the spectrum of morphology available to us in the fossils. We suggest that, in the absence of any synapomorphies linking ausktribosphenids with other mammalian groups, these characters be regarded as uniting ausktribosphenids with the Placentalia.

Particularly in light of the discovery of MSC 145, which happened after Kielan-Jaworowska *et al.* (1998) wrote their analysis of *Ausktribosphenos nyktos*, the objections they raised to its being a placental do not appear substantial enough to reject that hypothesis at this time. Certainly the discovery of an upper dentition of an ausktribosphenid would go far towards resolving this debate. That remains of four mammalian lower dentitions, all of the size to be ausktribosphenids, have now been found at the holotype locality of *A. nyktos*, gives a realistic prospect of an upper dentition eventually being recovered from there. While *A. nyktos* as a placental challenges a view dating back at least to Darwin and Wallace (Rainger 1991) that placentals arose in the northern hemisphere and spread to the southern, for biogeographic hypotheses not to be circular identifications of fossils must be made on the basis of their morphology alone. Their geologic age and geographic location are not legitimate considerations in their identification.

Fig. 1. Right dentaries rendered to approximately the same length, medial views. □A. Synapsid *Diarthrognathus*. □B. Early Jurassic primitive mammal or advanced synapsid *Morganucodon.* □C. Early Cretaceous placental *Prokennalestes.* □D. Early Cretaceous *Ausktribosphenos.* □E. MSC 145 [= NMV P208228], second specimen of an ausktribosphenid from the same locality as the holotype of *Ausktribosphenos nyktos.* □F. Late Cretaceous placental *Asioryctes.* Note the well-developed angle on the second ausktribosphenid (E), which is similar in position to that in *Asioryctes* (F). The position of the remnant of the angle that is preserved on the holotype of *Ausktribosphenos nyktos* (D) is indicated. The short, unlabelled arrows indicate the position of the mandibular foramen. Note, too, that the position of the angle in the Early Cretaceous placental *Prokennalestes* (C) is intermediate between that in the synapsid *Diarthrognathus* (A) and the synapsid or primitive mammal *Morganucodon* (B), on the one hand, and those in the Early Cretaceous ausktribosphenids (D–E) and the Late Cretaceous placental *Asioryctes* (F), on the other.

bosphenids. T.R. wishes to thank Zofia Kielan-Jaworowska for her hospitality during a visit to Poland, where he was able to discuss these matters at first hand and examine specimens of *Prokennalestes* and *Morganucodon*. For technical assistance with the production of this reply, we thank Ms. Draga Gelt and Ms. Patti Littlefield.

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